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THE INTERACTION OF GENES IN LEBISTES RETICULATUS

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Received August 26, 1947

THIS paper continues studies begun by GOODRICH *et al.* (1944) on the cellular analysis of certain genetic characters in *Lebistes reticulatus* (Peters). In the first paper the chromatophore patterns of two new autosomal recessive characters, blond and golden, and the double recessive, cream, were compared with the pattern of the wild type. Here a study is made of the effect of combining the maculatus gene with these autosomal genes. Maculatus was first noted by SCHMIDT (1920) and named with further description by WINGE (1922). This gene is carried by the Y chromosome and its most distinctive phenotypic effect is a conspicuous black spot on the dorsal fin of the male.

MATERIALS AND METHODS

Our stocks were supplied by kindness of C. P. HASKINS who had obtained them from WINGE. The stock we have used is also recorded as carrying the genes coccineus and vitellinus which are sex-linked ($CoVi_zMa_y$). These have been maintained in mass culture which has been necessary in order to provide sufficient numbers for experimental work. We also obtained a stock carrying maculatus only (O_zMa_y). But this has not supplied sufficient material for our use. SCHMIDT (1920) described the maculatus character as a "large black spot set in yellowish white." WINGE (1922) further noted the presence of a large red side spot below and in front of the dorsal fin and a black anal dot. Our analysis has been largely confined to a study of the cellular composition of the spot on the dorsal fin.

Our method has been to introduce the maculatus gene by appropriate crosses into the wild, blond, golden and cream stocks. The phenotypes were then studied and the presence of the maculatus gene was later confirmed by crosses to the wild stock. In all such cases the spot on the dorsal fin reappeared showing all typical characteristics. The details of these crosses are summarized in the accompanying table. As maculatus is a Y chromosome character only males are listed among the offspring.

DESCRIPTION OF PHENOTYPES

The characteristic wild (*B G* or + +), blond (*b G* or *b* +), golden (*B g* or + *g*) and cream (*b g*) are controlled by autosomal independently segregating genes (GOODRICH *et al.* 1944) It is important to note that the melanophores in these three types vary in size, form and number. The purpose of our experiments was to discover how the maculatus gene utilizes or reacts with the cell types controlled by the autosomal genes. A description of each phenotypic combination follows.

TABLE 1

RECORD NUMBER	CROSS	TOTAL YOUNG	MALES MATURING
517	wild maculatus ♂×normal wild ♀ +/+ +/+ O_z/ma_y×+/+ +/+ O_z/O_z	26 wild	8 wild maculatus (1) +/+ +/+ o_z/ma_y
542	(1) ×normal wild ♀ +/+ +/+ O_z/ma_y×+/+ +/+ O_z/O_z	21 wild	10 wild maculatus +/+ +/+ O_z/ma_y
519	wild maculatus ♂×blond ♀ +/+ +/+ O_z/ma_y×b/b +/+ O_z/O_z	30 wild	15 wild maculatus (2) +/b +/+ O_z/ma_y
522	(2)×blond ♀	82 wild	31 wild maculatus
523	+/b +/+ O_z/ma_y×b/b +/+ O_z/O_z	80 blond	+/b +/+ O_z/ma_y 44 blond (maculatus) (3) b/b +/+ O_z/ma_y
	(3) ×normal wild ♀	65 wild	
529			27 wild maculatus
533			
541	b/b +/+ O_z/ma_y×+/+ +/+ O_z/O_z		+/b +/+ O_z/ma_y
518	wild maculatus ♂×golden ♀ +/+ +/+ O_z/ma_y×+/+ g/g O_z/O_z	35 wild	15 wild maculatus (4) +/+ +/g O_z/ma_y
533, 534	(4) ×golden ♀	21 wild	11 wild maculatus
537, 538		37 golden	+/+ +/g O_z/ma_y
543	+/+ +/g O_z/ma_y×+/+ g/g O_z/O_z		16 golden (maculatus) +/+ g/g O_z/ma_y (5)
539	(5) ×normal wild ♀ +/+ g/g O_z/ma_y×+/+ +/+ O_z/O_z	76 wild	13 wild maculatus +/+ +/g O_z/ma_y
520	wild maculatus ♂×cream ♀ +/+ +/+ O_z/ma_z×b/b g/g O_z/O_z	15 wild	6 wild maculatus (6) +/b +/g O_z/ma_y
525, 526	(6) ×cream ♀	38 dark	6 wild maculatus
527		59 light	+/b +/g O_z/ma_y 6 blond b/b +/g O_z/ma_y 2 golden +/b g/g O_z/ma_y 1 cream b/b g/g O_z/ma_y (7)
556	(7) ×wild ♀ b/b g/g O_z/ma_y×+/+ +/+ O_z/O_z	80 wild	10 wild maculatus +/b +/g O_z/ma_y

Maculatus combined with wild

The dorsal fin of the wild type shows characteristic rosette type melanophores averaging from 70 to 120 micra in diameter. These are distributed so that although cell processes may be in contact the individual cells are clearly distinguishable (fig. 1).

When maculatus is introduced a dense accumulation of melanophores forms a spot covering from one half to three quarters of the area of the dorsal fin (fig. 2). Histological sections show this to be several cell layers in thickness in contrast to the single layer of melanophores of the wild type. The cells are so crowded that cell boundaries are merged. Even when the pigment is concentrated by treatment with adrenalin only a few peripheral cells become individually distinguishable. The melanophores appear to be both larger and more numerous than in the wild non-maculatus type. The black spot is surrounded by an area crowded with xanthophores and iridocytes. The presence of large numbers of xanthophores may be due to the coccineus vitellinus complex present in these crosses as noted above. By transmitted light this zone appears deep yellow but by reflected light it is bright bluish green.

Maculatus combined with blond

The dorsal fin of the blond type carries small rounded or "punctate" melanophores from nine to 15 micra in diameter (fig. 3). These are relatively evenly distributed and never form cell processes of any sort. It will be noticed in the table that when the male *No.* 2, heterozygous for wild and blond and carrying maculatus in the Y chromosome, is crossed with a blond female two male phenotypes are found as expected—the wild showing the maculatus spot and the blond without it. In this blond form there is no aggregation of melanophores of any type (fig. 4). Frequently, however, there is a massing of xanthophores and iridoctyes in from one to three areas and melanophores are largely absent in these spots. There is such an area toward the middle of the right side of the fin in figure 4. A red spot on the side of the body is similar to that associated with maculatus but the anal dot is absent. WINGE (1922) noted that in the wild maculatus this dot was sometimes "invisible."

Maculatus combined with golden

In the golden the coralla type melanophores of the body region are larger and less numerous than in the wild form. On the dorsal fin, however, they seem to vary from 70 to 130 micra in diameter indicating that they are about the same size as in wild. The distribution on the body is most irregular, producing a variegated pattern. This condition also extends to the dorsal fin where the melanophores tend to accumulate in clusters, which sometimes (fig. 5) resemble the maculatus spot. When however the maculatus gene is introduced no change is produced. There is merely the same variability as in the golden type. Figure 6 which shows the fin from a fish carrying the maculatus gene is well within the range of variations of the golden without maculatus. Some with maculatus had no spots. The suppression of the maculatus spot was noted by HASKINS and DRUZBA (1938) who stated that the factor Fredlini (later identified as our golden) inhibited the expression of the maculatus gene. Some counts have indicated that there may be a smaller number of melanophores than in the ordinary golden type. Xanthophores and iridocytes are localized in the lower anterior quarter of the fin. Both the red spot and anal dot are pres-

ent on the side of the body. As in the case of blond the table shows two classes of males, wild maculatus and golden, appearing in the backcross with golden.

Maculatus combined with cream

Cream results from the presence of both golden and blond. The melanophores are few in number and chiefly of the punctate type. This is a very nonviable type and it has been difficult to carry through crosses to demonstrate the effect of the maculatus gene. In one case, however, it has been carried to completion and the progeny tested (see table 1). In this case the backcross of the heterozygous wild maculatus (6) with a cream female is expected to give four classes which were all realized but not in equal numbers probably due in part to differential viability. No effect of the maculatus gene while present in cream has been noted on the dorsal fin. The red spot, however, appears on the side of the body.

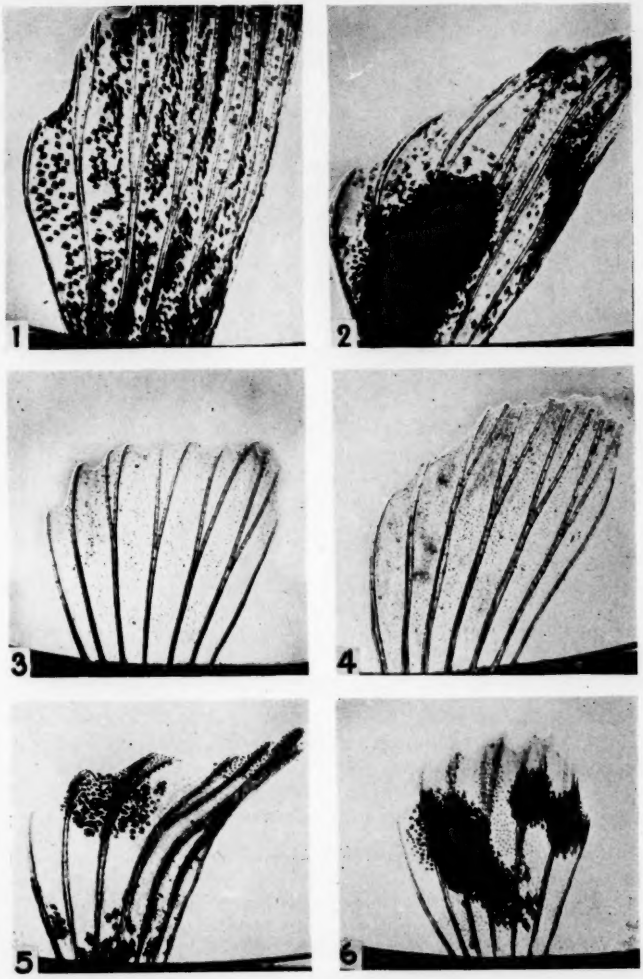
HORMONE EXPERIMENTS ON MACULATUS

A limited number of tests were made similar to those of previous investigators (see review by REGNIER 1938, and subsequent papers by BERKOWITZ 1937, 1938, 1941) to determine the relation of the maculatus spot to sex hormones. Female hormone (estradiol) was fed to the young of a litter from wild maculatus stock. All eight that survived to maturity showed female characteristics and no maculatus markings. The feeding of the hormone was then discontinued and two assumed male characteristics and the maculatus spot appeared. Thus it was indicated that in this litter there were six genetic females and two genetic males. The upper half of the dorsal fin of an adult male which was being fed with the female hormone was removed by a cut through the maculatus spot. The spot did not re-form when the fin regenerated above the cut and the part remaining below disintegrated.

The male hormone (methyl-testosterone) was similarly fed to a litter of young and at maturity all surviving were male. Of these some showed the spot which was absent in others. This result would of course be expected as the female genotypes would not carry the maculatus gene. Male hormone was fed to adult females of the maculatus stock. There was some disintegration of melanophores in the dorsal fin and brighter colors appeared but no formation of a spot. When male hormone was fed to adult males not carrying maculatus there was a deepening of colors but no formation of a spot. These tests seem to confirm the hypothesis that the female hormone suppresses the development of the maculatus spot and that possibly the male hormone is necessary for its formation.

DISCUSSION

The blond maculatus phenotype appears intermediate so far as the spot is concerned between the combinations with wild and with golden. The melanophores are not massed but the locus of the spot appears marked by an assemblage of xanthophores and iridocytes. This suggests that some morphogenetic factor may be in operation but that it does not utilize the type of melanophores



DESCRIPTION OF PLATE

Photomicrographs of dorsal fins magnified about ×14 are here reproduced. Unfortunately it has not been possible to obtain all fins of the same degree of development and all similarly expanded. Also figure 5 shows an unusual form, probably due to a genetic modification, but the markings are typical.

FIGURE 1.—Wild.

FIGURE 2.—Wild maculatus.

FIGURE 3.—Blond.

FIGURE 4.—Blond maculatus. Lighter region right of center is area occupied by iridocytes that are only visible by reflected light.

FIGURE 5.—Golden—one variation.

FIGURE 6.—Golden maculatus—one variation.

that are available. It is hoped that studies in progress on the development and regeneration of the maculatus spot may give some information about factors that are involved. It appears, however, that the maculatus gene and those dominant to blond and to golden and the proper balance of hormones to control the secondary male sex characters must all be present to produce the maculatus spot.

We have noted that our maculatus stock carried the coccineus vitellinus genes (WINGE 1922). The principal effect on the dorsal fin is to produce more xanthophores. While this should be borne in mind we do not feel that it vitiates our essential results.

SUMMARY

1. Maculatus, a Y chromosome gene of *Lebistes reticulatus* which in the wild type produces a black spot on the dorsal fin, has been crossed into mutant stocks having different body color patterns of chromatophores controlled by autosomal genes.

2. Maculatus combined with blond produces no spot on dorsal fin but there is an aggregation of iridocytes and xanthophores.

3. Maculatus combined with golden produces no effect on the dorsal fin.

4. Hormone tests have been made which indicate that the female sex hormone can suppress the maculatus spot and that the male hormone may be necessary for its development.

5. The maculatus gene, the genes dominant to blond and golden, and the male sex determiners must be present to permit development of the maculatus spot.

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CHROMOSOME NUMBERS IN CROSSES OF DIPLOID, TRIPLOID AND TETRAPLOID MAIZE

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INTRODUCTION

THE spontaneous occurrence of triploidy in diploid stocks of maize has been observed at infrequent intervals (RANDOLPH and MCCLINTOCK 1926, RHOADES 1936), but tetraploidy has never been reported in untreated stocks of maize. Triploids presumably arise through the functioning of a normally reduced gamete in combination with a gamete containing the unreduced number of chromosomes. Because of the infrequency with which triploidy occurs, the probability is very remote that tetraploidy would occur in a similar manner through the random mating of two exceptional gametes with the diploid number of chromosomes, expecially as diploid pollen cannot compete favorably with haploid pollen in either diploid or tetraploid styles (RANDOLPH, 1935). Furthermore, the maize plant is monoecious and almost exclusively cross-pollinated, which would limit appreciably the possibility of tetraploids arising from somatic chromosome doubling.

The experimental production of tetraploids by heat treatment applied to the dividing zygote and proembryo (RANDOLPH 1932) furnished abundant materials for a study of the characteristics of tetraploid maize (RANDOLPH 1935, FISCHER 1939, KADAM 1940) and also provided material from which triploids could be obtained by intercrossing diploids and tetraploids.

Tetraploids derived by direct chromosome doubling of inbred lines of maize are much less vigorous and more highly sterile than are tetraploids originating from vigorous hybrid combinations of inbred lines. For this reason foundation stocks for the present study were selected from hybrids involving various inbred lines. The diploid and tetraploid stocks originated from a hybrid combination of diploid lines of Webers Dent, Illinois A and Luces Favorite. This hybrid was doubled with heat to produce a strain of tetraploid maize which was propagated for seven generations in an open-pollinated, isolated plot and selected for high fertility. These foundation stocks of diploids and tetraploids were supplied by PROFESSOR RANDOLPH for the experiments, which were conducted at CORNELL UNIVERSITY in 1940 and 1941 and completed at DUKE UNIVERSITY in 1942.

The crosses made during the progress of this investigation were carefully controlled by hand pollination to limit the possibility of contamination. Due to the prevalence of defective seeds from which it is often difficult to obtain viable seedlings following crosses between members of a polyploid series, sterile conditions were maintained in germinating the seeds, and when necessary the nutrient solution of HOAGLAND and ARNON (1938) was employed to stimulate the growth of the seedlings.

Root-tips were fixed in RANDOLPH'S CRAF solution and infiltrated with paraffin according to his schedule. In the early period of the investigation, the crystal-violet staining procedure developed by RANDOLPH was followed. Later, however, a modification of the crystal-violet-iodide technique of SMITH (1934) was used. The slides were mordanted in the iodine and potassium iodide solution overnight instead of 10 to 20 minutes as suggested by SMITH. They were then stained in a one percent aqueous solution of crystal-violet for four hours, rinsed in water, and dipped in two percent acetic acid for one second. After being rinsed in water again, they were again mordanted in a solution of iodine and potassium iodide dissolved in 80 percent alcohol, passed quickly through 95 percent alcohol, absolute alcohol containing picric acid, and then pure alcohol. Finally, they were differentiated in clove oil and mounted in balsam. For meiotic studies, microsporocytes were fixed in three parts absolute alcohol and one part glacial acetic acid, stored in a refrigerator until ready for use, and stained according to BELLING'S iron-aceto-carmine method.

In the analyses of chromosome behavior, FISHER'S statistical methods were employed in calculating means and standard deviations. The significance of differences was determined by the "t" values. Occasionally, FISHER'S Analysis of Variance was followed, especially in cases with unequal observations, such as those involving pollen fertility and percentage of seed set. In the interpretation of the data, probability values of five percent or less were regarded as significant.

DIPLOID AND TETRAPLOID INTERCROSSES

The crossability of naturally occurring, intraspecific diploids and tetraploids has been studied in many species of plants. In 1936 MÜNTZING published a list of fourteen species, including both dicotyledons and monocotyledons, in which $2n \times 4n$ crosses and their reciprocals were made, and numerous additional cases have been reported more recently. All showed a remarkable incompatibility varying in degree from high to absolute. In experimentally induced autotetraploids, as Zea (RANDOLPH 1935) and Cucumis (SHIFRISS 1942), incompatibility ordinarily is pronounced. But exceptions do occur, as in Populus (JOHNSON 1945) in which there was only light incompatibility.

In Zea, RANDOLPH found that when the diploid was used as the seed parent, fertility as measured by the proportion of viable to non-viable seeds was less than 0.5 percent, whereas in the reciprocal cross it was somewhat higher, ranging from three to five percent. RANDOLPH also noted irregularities in chromosome distribution at meiosis in tetraploids and reported that tetraploid populations did not breed true for the balanced euploid number of 40 chromosomes. Somatic chromosome numbers varied from 37 to 42. The microspores of the tetraploid were found by FISHER (1939) to have numbers ranging from 14 to 24. In the present study chromosome numbers were determined by root-tip counts in reciprocal $2n \times 4n$ crosses involving tetraploid plants with 40 chromosomes and normal diploid plants with 20 chromosomes. The counts included all of the viable seedlings from 12 ears of the $2n \times 4n$ cross and 21 ears of the $4n \times 2n$ cross and are summarized in table 1.

TABLE 1

Somatic chromosome numbers in the F_1 progenies of intercrosses between diploid and tetraploid maize.

TYPE OF CROSS AND PERCENT	CHROMOSOME NUMBERS IN F_1 PROGENIES									TOTAL
	26	27	28	29	30	31	32	33	34	
$2n \times 4n$		4	13	21	81	4	1			124
Percent		3.23	10.48	16.94	65.32	3.23	0.80			100
$4n \times 2n$	1	3	49	84	178	34	14	5	1	369
Percent	0.27	0.82	13.28	22.76	48.24	9.21	3.79	1.36	0.27	100

Meiosis in the diploids used in these crosses was perfectly regular with respect to the assortment of the chromosomes and it may be assumed that they formed ten-chromosome gametes with a high degree of regularity. Therefore, numbers other than 30 appearing in the F_1 progeny of these $2n \times 4n$ crosses may be attributed to variation in the gametic chromosome number of the tetraploid parent. Numbers ranging from 27 to 32 were noted among 124 F_1 plants having the diploid as the seed parent; of these 65 percent had 30 chromosomes. When the tetraploid was the seed parent only 48 percent of the 369 plants examined had 30 chromosomes and the range of numbers observed was extended to 26 at one extreme and 34 at the other. This greater range presumably was due to the fact that more plants were examined in the latter case.

The chromosome numbers in the progeny of the $4n \times 2n$ cross corresponded very closely to the numbers expected from what is known concerning the meiotic assortment of the chromosomes to the microspores in the tetraploid, as reported by FISCHER (1939) and reproduced in table 2.

There is no evidence of either gametic selection or differential viability of the zygotes, an unexpected result in view of the very low percentage of seed set on the parent ears. The data indicate that the pronounced cross incompatibility of diploid and tetraploid maize is not affected by the variation in the gametic chromosome numbers of the tetraploid.

TABLE 2

Microspore chromosome counts of tetraploid maize (Data from FISCHER, 1939).

LINE	CHROMOSOME NUMBERS OF MICROSPORES											TOTAL
	14	15	16	17	18	19	20	21	22	23	24	
1F	1	1	5	8	14	27	69	15	7	4		153
10S	1	2	10	13	10	17	51	19	11	6	6	146
30872 41-4				1	6	7	22	1				37
Total	2	3	15	22	30	51	142	35	18	10	6	336
Percent	0.60	0.88	4.45	6.55	8.93	15.18	42.26	10.42	5.35	2.97	1.78	100

There is definite evidence of gametic selection in the reciprocal $2n \times 4n$ cross. A much higher proportion of the progeny are balanced 30-chromosome triploids when the cross is made in this direction. Presumably, pollen tubes carrying the balanced diploid number of chromosomes did not increase the proportion of viable seeds; in fact the reverse was true.

When the tetraploid was the seed parent a proportionately higher number of gametes with unbalanced chromosome numbers functioned in the absence of the competitive action of pollen tubes to produce more aneuploids than were produced in the reciprocal cross. Only 48 percent of the progeny were 30-chromosome triploids, while in the reciprocal cross 65 percent were triploid.

There is no evidence either from the direct or reciprocal diploid-tetraploid crosses that the very low percent of viable seed resulting from these crosses is to be attributed to the non-functioning of gametes with more unbalanced chromosome numbers. In fact, the chromosome numbers observed in the progeny of the $4n \times 2n$ cross corresponded very closely to expectations based on the microspore counts of the tetraploid. Whatever the factors may be that are responsible for the pronounced cross incompatibility of diploid and tetraploid maize, they seem to have a similar effect on the various gametic combinations resulting from the cross.

MEIOSIS IN TRIPLOID MAIZE

The formation of gametes with varying numbers of chromosomes by triploids and other autoploids provides a favorable opportunity to study the relation of various aneuploid chromosome numbers to cross incompatibility due to differences in chromosome number.

Triploid maize was observed by RANDOLPH and MCCLINTOCK (1926) and MCCLINTOCK (1929) to form varying numbers of trivalents ranging from six to ten, and from zero to four bivalents and univalents. In the present study among 216 microsporocytes examined at diakinesis and metaphase I there were 106 with ten trivalents, 66 with nine, 35 with eight, 8 with seven, and 1 with six, the mean number being 9.24 ± 0.89. The presence of from one to four univalents in approximately 50 percent of the cells and the random two-from-one assortment of the trivalents resulted in unequal disjunction and irregular distribution of the chromosomes. Varying numbers of lagging chromosomes were noted in 143 of the 559 cells examined at this stage, from one to four laggards being present in each cell. The mean number of lagging chromosomes at these stages were 0.424 ± 0.036. Fewer lagging chromosomes per cell were noted in the anaphase and telophase stages of the second division. Of 479 cells examined there were 389 with no laggards, 72 with one, 15 with two, 1 with three and 2 with four, the mean value being 0.236 ± 0.025. This was a significant difference, the "t" value of the difference in the two means for the first and second division being 4.286. At the quartet stage, only 43 of 404 microspores that were examined had a visible remnant of a lagging chromosome, which in some cases formed a micronucleus. Only two cells with two chromosome remnants were seen at this stage. The mean value for the microspores was 0.116 ± 0.017. This value is approximately one-half the value observed at the close of the second division

and it in turn is very close to one-half of the value obtained for the anaphase and telophase stages of the first division. This is the expected frequency based on the assumption that the chromosomes eliminated during the first division persisted in the cytoplasm of the dyads and microspores and no additional elimination or disappearance of previously eliminated chromosomes occurred during the second meiotic division. The observed behavior of the chromosomes supported this interpretation.

CHROMOSOME NUMBERS IN MICROSPORES OF THE TRIPLOID

Because of the irregularities in chromosome assortment encountered in the meiotic process of triploid maize, one would naturally expect considerable variation in the chromosome numbers of the microspores. The results shown in table 3 were obtained from an examination of the late prophase and early metaphase of the first meiotic division of the microspores.

TABLE 3

Chromosome numbers in the microspores of triploid maize ($2n=30$).

SOURCE OF TRIPLOIDS	NUMBER OF EARS	CHROMOSOME NUMBER IN MICROSPORES										TOTAL
		10	11	12	13	14	15	16	17	18	19	
($2n \times 4n$)	4	15	62	140	190	225	272	128	56	23	—	IIII
($4n \times 2n$)	14	26	77	204	348	415	546	257	132	56	15	2076
Total		41	139	344	538	640	818	385	188	79	15	3187
Percent		1.29	4.36	10.79	16.88	20.08	25.67	12.08	5.90	2.48	0.47	100

Significantly, the chromosome distribution in the microspores closely resembled that of a normal population curve with the mode at $n=15$. However, there were fewer spores with more than 15 chromosomes than there were with less than 15 chromosomes, the mean being 14.23 ± 1.71. The observed elimination of chromosomes in meiosis explains this difference, which is represented graphically in figure 1. Megasporogenesis and megaspore chromosome numbers were not investigated but there is no *a priori* reason to assume that the numbers observed in the megaspores differed appreciably from those observed in the microspores.

Although there was a very noticeable difference in the size of the pollen grains formed by the triploid, from 85 to 97 percent of the mature grains were normal in appearance and were well filled with starch. Whether or not the empty and shrivelled pollen grains, which comprised from 3 to 15 percent of the total, originated from microspores with the more unbalanced chromosome numbers is not known. However, the occurrence of this low percentage of bad pollen should be considered in interpreting the selective functioning of the pollen and eggs of the triploid, which was evident in the results of crosses to be described later.

DIPLOID AND TRIPLOID INTERCROSSES

From relatively small numbers of chromosome counts of direct and reciprocal $2n \times 3n$ crosses McCLINTOCK (1929) noted that when the triploid was the

seed parent more extra chromosomes were transmitted to the progeny than when the triploid was the pollen parent (table 4).

All of the ears resulting from the crosses were poorly filled, suggesting to her that many of the gametic combinations were inviable. In the present study much larger numbers of individuals were involved and when combined with McCLINTOCK's data the results demonstrate that the direct and reciprocal crosses differ very significantly with respect to the numbers of extra chromosomes in the F_1 progeny. In the $2n \times 3n$ cross 66 percent of the plants had no extra chromosomes and 22 percent had but one extra chromosome. Male gametes of the triploid which had more than 10 or 11 chromosomes rarely functioned in combination with the ten-chromosome female gametes of the diploid. When the triploid was the seed parent 56 percent of the progeny had

TABLE 4

Somatic chromosome numbers in the F_1 progenies of the intercrosses between diploids and triploids and their reciprocals.

TYPE OF CROSS	NO. OF EARS	CHROMOSOME NUMBERS OF F_1 PROGENIES											TOTAL
		20	21	22	23	24	25	26	27	28	29	30	
$2n \times 3n$	7	27	6	3	—	—	—	—	—	—	—	1	37*
	6	136	49	9	2	—	2	—	2	9	—	—	209
Total		163	55	12	2	—	2	—	2	9	—	1	246
Percent		66.26	22.36	4.88	0.81	—	0.81	—	0.81	3.66	—	0.41	100
$3n \times 2n$	2	—	2	4	2	3	1	—	1	—	—	—	13*
	7	5	32	84	71	49	22	7	1	—	—	—	271
Total		5	34	88	73	52	23	7	2	—	—	—	284
Percent		1.76	11.97	30.99	25.70	18.32	8.10	2.46	0.70	—	—	—	100

* Data of McCLINTOCK (1929).

either 22 or 23 chromosomes, only 12 percent had 21 chromosomes, and less than two percent had 20 chromosomes.

In the $2n \times 3n$ cross there was very definite evidence of the selective elimination of pollen grains with more than one extra chromosome and a pronounced tendency for gametes with no extra, or only one extra chromosome to function. Of the 246 F_1 plants whose chromosomes were counted 66.26 percent had 20 chromosomes, although only 1.29 percent of the 3187 microspores of the triploid parent had ten chromosomes. In the triploid 25.67 percent of the microspores had 15 chromosomes, but only 0.81 percent of the F_1 plants had 25 chromosomes. There is close agreement between the observed and expected numbers only in the case of the 18-chromosome gametes and 28-chromosome plants, the former occurring with a frequency of 2.48 percent, according to the microspore count, and the latter with a frequency of 3.66 percent.

The tendency for most of the F_1 plants from the $2n \times 3n$ cross to have either 20 or 21 chromosomes, with an indication that the number 28 is favored over the intermediate numbers from 22 to 27, is attributable primarily to a slower

rate of growth of pollen tubes with numbers of extra chromosomes intermediate between 10 and 20, since a much higher proportion of the plants with extra chromosomes appeared in the progeny of the reciprocal cross in which pollen tube competition was lacking.

The ears from the *2n*×*3n* crosses were poorly filled and many of the seeds were only partly developed. To test the possibility that zygotes with more than one or two extra chromosomes may have been produced but failed to develop into viable seeds, the seeds from the *2n*×*3n* crosses were sorted into two classes, large and small, and their chromosome numbers were determined from seedling root-tip counts. The results are shown in table 5.

TABLE 5

Somatic chromosome numbers in the seedlings produced by the small and large seeds from the 2n×3n crosses.

SEED SIZE	CHROMOSOME NUMBERS									TOTAL	MEAN
	20	21	22	23	24	25	26	27	28		
Large	57	14	4			1				76	20.36±0.01
Small	22	19	2	1				2	4	50	21.44±0.34

The mean chromosome numbers of the seedlings obtained from the large and small seeds were significantly different. However, much of this difference was due to different frequencies of 20- and 21-chromosome plants, and seeds containing embryos with 21 chromosomes are known to germinate about as well as those with 20 chromosomes. Thus there is little evidence from these data that zygotic elimination appreciably influenced the results of the *2n*×*3n* cross.

The results of the reciprocal *3n*×*2n* cross indicated that zygotic lethality was a significant factor in determining frequencies of various chromosome numbers in the progeny of this cross. The female gametes of the triploids that functioned to produce viable seedlings apparently had chromosome numbers somewhat lower on the average than those observed in the microspore divisions of the triploid. By deducting ten, the chromosome number contributed by the pollen, from the F_1 mean of 22.85±1.33, the value 12.85 is obtained for the mean chromosome number of the functioned eggs. This is significantly lower than the mean chromosome number 14.23 in the microspores.

Evidence that the difference between these two values was due to zygotic lethality during kernel development was obtained from an analysis of chromosome numbers in seedlings produced by the small, medium and large seeds resulting from the *3n*×*2n* cross (table 6).

The seedlings produced by the small seeds had a higher mean number of chromosomes than did those obtained from the large seeds. Those from medium sized seeds had a mean chromosome number that was intermediate between the values for the seedlings from the large and small seeds. Furthermore, many of the small and medium sized seeds failed to germinate, while most of the large seeds germinated very well. The reduced germination of the smaller seeds

TABLE 6

Somatic chromosome numbers in the seedlings produced by the small, medium and large seeds resulting from the 3n×2n cross.

SEED SIZE	CHROMOSOME NUMBERS									TOTAL	MEAN
	20	21	22	23	24	25	26	27	28		
Large	4	24	34	14	10	1				87	22.06±0.12
Medium		4	25	43	32	15	2			121	23.29±0.10
Small			2	13	33	26	28	6	1	109	24.80±0.12

with relatively high chromosome numbers accounted for the fact that mean number of chromosomes in the *3n×2n* seedling frequencies was somewhat lower than expected, assuming that the female gametes of the triploid seed parent contributed to the cross chromosome numbers that were the same as those observed in the microspore divisions of the triploid.

TRIPLOID AND TETRAPLOID INTERCROSSES

When pollen of the triploid was applied to silks of the tetraploid there was the same tendency, encountered in the *2n×3n* cross, for gametes with chromosome numbers approaching the diploid and also to a limited extent the haploid numbers to function more frequently than did those with intermediate numbers (table 7).

In this case, however, pollen grains carrying the higher numbers of chromosomes were definitely favored; only 4.88 percent of the 123 plants examined from the *4n×3n* cross had from 29 to 31 chromosomes. The others had numbers ranging from 35 to 42, and 35.77 percent of the total had 40 chromosomes. The deviations from 40, especially in the plus direction, undoubtedly were due in part to the variation in the number of chromosomes contributed by the eggs of the tetraploid, as shown by the results of the *2n×4n* cross previously described. Comparison of the gametic chromosome numbers of the triploid which functioned in the *2n×3n* and *4n×3n* crosses leads to the conclusion that in these crosses the chromosome number of the seed parent was the most important factor determining whether male gametes with low or high numbers of chromosomes would function.

TABLE 7

Somatic chromosome numbers in the F_1 progenies of 11 intercrosses between triploids and tetraploids and eight of their reciprocals.

TYPE OF CROSS	CHROMOSOME NUMBERS OF F_1 PROGENIES														TOTAL
	29	30	31	32	33	34	35	36	37	38	39	40	41	42	
4n×3n	3	2	1	—	—	—	1	6	9	25	22	44	5	5	123
Percent	2.44	1.63	0.81	—	—	—	0.81	4.88	7.32	20.33	17.89	35.77	4.06	4.06	100
3n×4n	—	—	—	3	10	13	22	27	15	13	5	4	1	—	113
Percent	—	—	—	2.65	8.86	11.51	19.47	23.89	13.27	11.50	4.43	3.54	0.88	—	100

The chromosome numbers in the F_1 progeny of the $3n \times 4n$ cross were mostly intermediate between the triploid and tetraploid numbers. The frequency distribution of chromosome numbers in this cross was definitely unimodal and resembled that of the gametes of the triploid, as indicated by the microspore counts of the triploid (table 3). However, the trend was somewhat away from the expected in the direction of the tetraploid number.

The high proportion of 40-chromosome plants, resulting from the $3n \times 4n$ cross and the occurrence of several plants with more than 40 chromosomes, as well as a considerable number with only one or two chromosomes less than 40 is especially noteworthy in view of the fact that the microspore chromosome counts of the triploid are not high enough to account for the observed results (table 3). Among the 3187 microspores of the triploid that were examined, there were none with 20 or more chromosomes and very few with 19 chromosomes. Since the tetraploid produces gametes with variable numbers of chromosomes, ranging from 14 to 24 (table 2), gametic selection favoring a union of the higher numbers from both parents may have been involved. Or, nondisjunction of individual chromosomes in the division of the generative nucleus of the maturing pollen of the triploid may have produced functional male gametes with chromosome numbers consistently higher than those present in the microspores. However, there was no evidence of this in the $2n \times 3n$ cross, in which the triploid also was involved as the male parent.

TRIPLOID SELFED

Triploid maize would not be expected to breed true for chromosome number because of irregularities in synapsis and disjunction associated with the presence of three sets of ten homologous chromosomes. Its behavior in this respect exceeded expectations. There was not only a wide range of chromosome numbers represented among the progeny of selfed triploids, but individuals with 30 chromosomes were extremely rare (table 8). Only 7 of the 300 F_1 plants that were counted had 30 chromosomes.

These data were obtained from 43 triploids that had been self-pollinated under carefully controlled conditions to minimize the possibility of contamination. It was definitely established from root-tip chromosome counts that 21 of these triploid plants had 30 chromosomes and the remaining two had either 30 or approximately 30 chromosomes.

The distribution of the 300 F_1 plants that were counted, with respect to their chromosome number, was bimodal. The numbers varied from 20 to 38, with a greater concentration in the lower than in the higher range of numbers. Assuming that chromosome behavior was the same in microsporogenesis and megasporogenesis, and that there were no post-meiotic irregularities in chromosomal assortment, the male and female gametes of triploids should have similar chromosome numbers, and these numbers should be essentially the same as those observed in the first division of the microspores (table 3).

As previously noted, there was apparently no selection of eggs with particular chromosome numbers either in the $3n \times 2n$ or the $3n \times 4n$ crosses, but the pollen of the triploid behaved differently. The pollen grains of the triploid

from the two extremes of the gametic range, which approached the haploid and diploid numbers, functioned in both the $2n \times 3n$ and $4n \times 3n$ crosses almost to the exclusion of the gametes with the intermediate numbers. Therefore, it was especially interesting to determine the behavior of the pollen of triploids on their own silks.

The conspicuous failure of triploid maize to breed true for chromosome number can be interpreted in the light of what is known concerning the gametic chromosome numbers of the triploid and the frequency with which different chromosome numbers were observed in the progenies of $3n \times 2n$ and $2n \times 3n$

TABLE 8

Somatic chromosome numbers in the F_1 progenies of 23 selfed triploid plants.

	CHROMOSOME NUMBERS									
	20	21	22	23	24	25	26	27	28	29
Total	5	18	26	46	50	33	18	16	8	3
Percent	1.67	6.00	8.67	15.33	16.67	11.00	6.00	5.33	2.67	1.00

	CHROMOSOME NUMBERS									
	30	31	32	33	34	35	36	37	38	TOTAL
Total	7	5	11	12	14	11	8	6	3	300
Percent	2.33	1.67	3.66	4.00	4.67	3.66	2.67	2.00	1.00	100

crosses. By combining the female gametic numbers of the triploid that obviously functioned in the $3n \times 2n$ cross and the male gametic numbers that functioned in the reciprocal $2n \times 3n$ cross with frequencies that prevailed in those crosses, the result would be very similar to the observed frequencies in the selfed progeny of the triploid, except that there were somewhat fewer plants with numbers intermediate between the diploid, triploid and tetraploid numbers than would have been expected. In this case as in the $3n \times 2n$ cross, the reduction in the number of plants with these intermediate numbers may have been due to zygotic lethal effects.

The seeds that were produced by the triploids following self-pollination were extremely variable in size. By determining the chromosome numbers of seedlings produced by the large, medium and small seeds, it was found that the large and medium size seeds produced about the same relative number of plants with chromosome counts ranging from 20 to 38, and their distribution was definitely bimodal (table 9).

TABLE 9

Somatic chromosome numbers in seedlings from the small, medium and large seeds in the triploid selfed.

SEED SIZE	CHROMOSOME NUMBERS																			TOTAL	MEAN
	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38		
Large	1	7	9	5	4	0	1	2	1	0	1	1	4	5	9	7	7	6	3	73	29.82±0.73
Medium	2	5	7	12	14	3	3	3	3	1	2	3	4	6	5	3	1	—	—	77	26.60±0.53
Small	—	—	4	17	22	21	11	9	3											87	24.66±0.16

The seedlings obtained from the small seeds had a unimodal distribution within the more limited range of 22 to 28 chromosomes and a mean of 24.66 ± 0.16. Unfortunately, the percentage of germination for the large, medium and small seeds was not recorded separately. Consequently, the extent to which selective viability of the seeds may have influenced the frequencies of various chromosome numbers in the progeny is unknown, but it is probable that seeds with numbers intermediate between the euploid numbers 20, 30 and 40 germinated more poorly than those with euploid or approximately euploid numbers, and reduced proportionately the number of seedlings in these classes.

The breeding behavior of triploid maize was similar to that reported by NISHIYAMA (1934) for triploid hybrids of Avena with respect to the recurrence of triploids after self-pollination. Among 124 plants in the selfed progeny of *A. barbata*×*A. strigosa* and *A. barbata*×*A. Wiestii* triploids there was only one triploid; most of the F_1 plants had numbers intermediate between the triploid and tetraploid numbers. In chives (*Allium Schoenoprasum*) there was a slight tendency for plants with the triploid number to appear more frequently than plants with one or two chromosomes more or less than the triploid number to appear more frequently than plants with one or two chromosomes more or less than the triploid number in the progeny of triploids, but most of the 619 plants counted by LEVAN (1936) had numbers more closely approximating the tetraploid number. The absence of triploids in the selfed progenies of maize triploids apparently was due to gametic selection favoring male gametes with chromosome numbers approximating the balanced numbers 10 and 20 and zygotic elimination early in ontogeny of individuals with chromosome numbers approximating the triploid number.

RELATION OF CHROMOSOME NUMBER TO POLLEN FORMATION AND SEED PRODUCTION

The fertility of heteroploid plants is conditioned by their ability to produce functional gametes and viable seeds. Data on pollen and seed production by plants wtih chromosome numbers ranging from 20 to 31 are summarized in table 10.

The pollen was classed as normal or aborted depending on whether the fresh grains were plump and well filled with starch or empty, shrivelled, or otherwise obviously incapable of performing their normal function. The percent of seed set of individual ears was computed by dividing the actual number of seeds produced, including well filled, partly filled and poorly filled seeds containing recognizable endosperm tissue, by the total number of ovules capable of producing seed.

There was considerable variation in the size of the pollen of the triploid but 92 percent of the grains were plump and well filled with starch. Under similar conditions 97 percent of the pollen produced by diploid plants was normal in appearance. The pollen of 21- and 31-chromosome plants with respect to the percent of well-filled grains was not significantly different from that of the diploid and triploid. However, the other aneuploids had signifi-

cantly lower percentages of good pollen, the 28-chromosome plants having only 65 percent which was the lowest value obtained for any of the plants.

With respect to their ability to produce seed following self-pollination, there was a strong negative correlation between the number of extra chromosomes and the percent of seed formed among the plants with 21 to 28 chromosomes. Only 3.63 percent of the ovules of 28-chromosome plants produced seed. Somewhat more seed was produced by the 29-chromosome plants, and 11 percent of the ovules of the triploid produced seed. The greatest unbalance relating

TABLE 10

Percentages of good pollen and seed produced by maize plants with 20 to 31 chromosomes.

CHROMOSOME NUMBERS	POLLEN CONDITION		SEED SET	
	PLANTS EXAMINED	PERCENT OF NORMAL POLLEN	EARS EXAMINED	PERCENT OF SEED SET
20	13	96.96±5.96	12	94.75±4.02
21	12	95.24±6.56	13	71.71±4.85
22	28	86.34±4.19	22	66.19±3.90
23	47	75.90±3.18	22	22.83±4.17
24	52	69.80±2.81	26	22.65±3.84
25	33	75.06±3.41	16	11.90±5.13
26	22	78.58±4.18	16	8.48±4.88
27	8	71.40±6.10	5	4.74±7.87
28	20	65.29±3.63	14	3.63±4.30
29	26	81.61±3.16	20	7.29±3.47
30	56	91.96±2.23	71	11.00±1.76
31	11	89.80±5.87	11	15.19±4.14

to both the condition of the pollen and the ability to produce seed was exhibited by plants with 28 chromosomes, rather thay by the 25-chromosome plants, as might have been expected. There is no simple explanation for this strange behavior. However, plants with one or two chromosomes less than the diploid number are very much lacking in vigor and fertility, while plants with one or a few chromosomes more than the diploid number are relatively much more vigorous and fertile. A similar relationship exists among $3n-1$ and $3n$ plants. This may explain why plants with 28 chromosomes were more unbalanced than those with numbers more nearly intermediate between the diploid and triploid numbers. In the triploid-tetraploid range where, in the cross $3n \times 4n$ (table 7), a more nearly normal frequency of distribution was observed, there is less evidence of a comparable unbalanced condition.

SUMMARY AND CONCLUSIONS

1. Triploids with 30 somatic chromosomes and aneuploids with chromosome numbers ranging from 26 to 34 are produced by intercrossing diploid and autotetraploid maize experimentally induced by heat treatment.

2. Chromosome numbers in the microspore division of the triploid varied

from 10 to 19 with a mean number of 14.23 ± 1.71, indicating that the gametic numbers are similarly variable.

3. The $3n \times 2n$ cross resulted in plants with from 20 to 27 chromosomes, the mean number being 22.85 ± 1.33. In the reciprocal cross 89 percent of the progeny had either 20 or 21 chromosomes. The difference between the two crosses with respect to chromosome numbers apparently was due primarily to pollen tube selection in the $2n \times 3n$ cross which strongly favored gametes with few or no extra chromosomes. Pollen tube competition was absent in the reciprocal cross and most of the progeny had chromosome numbers intermediate between the diploid and triploid numbers. In the $3n \times 2n$ cross the poor viability of defective seeds with two or more extra chromosomes reduced the number of viable seedlings with intermediate chromosome numbers.

4. In the direct and reciprocal crosses of triploid and tetraploid maize the chromosome numbers in the progeny more closely approached the tetraploid numbers when the tetraploid was the seed parent than when the triploid was the seed parent. The proportion of tetraploids and near tetraploids in the progeny of the $4n \times 3n$ cross was much higher than expected.

5. Triploid maize produced very few triploids when self-pollinated, most of the progeny being aneuploids with more or less than the triploid number of chromosomes. The breeding behavior of the triploid is interpreted on the basis of the results of the $2n \times 3n$ and $3n \times 2n$ crosses.

6. The relation of chromosome number to pollen formation and seed production in plants with from 20 to 31 chromosomes is considered briefly.

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THE OPTIMUM STRUCTURE OF BREEDING FLOCKS. I. RATE OF GENETIC IMPROVEMENT UNDER DIFFERENT BREEDING PLANS

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THE primary object of a breeder is to change the genetic composition of the population under his control so as to increase the proportion of more desirable genotypes in it at the expense of the less desirable ones. His ability to further this end is based on his power to determine which of the animals in his flock or herd are permitted to reproduce themselves, and to some extent in his regulation of the rate of reproduction of animals thus selected. The efficiency of the breeder's operations depends on three factors: 1) the intensity of selection, 2) the accuracy of selection, and 3) the average interval between generations (DICKERSON and HAZEL 1944).

The effect of the first of these factors is fairly obvious, since the improvement realized under selection is inversely related to the fraction of the population which is permitted to reproduce itself. If all of the members of a population leave offspring in equal numbers, no improvement will ensue. The more intense the selection is, the smaller the number of breeding animals selected will be, and, within the limits fixed by the effects of inbreeding, the greater the improvement in the trait selected for. There is a natural limitation to the increase in selection intensity, if a population of a constant or expanding size is desired, which is determined by the reproductive rate of the various domestic animals. Thus in the case of the domestic fowl, ordinarily about 10 to 20 percent of the females have to be selected to ensure maintenance of constant size of the flock. Intensity of selection may be measured either in terms of the fraction of the total population selected or in terms of the average superiority of the fraction selected above the average of the whole group (selection differential).

The second factor noted, that of accuracy of selection, may require a somewhat more extended discussion. Ordinarily the trait selected for is measured in phenotypic terms, that is to say in terms of its visible expression, rather than in terms of the genetic constitution for the character concerned. The variability of nearly all characters of economic importance in animals is, however, not entirely determined by the heredity of the animal but is also affected by the environment. Hence, only part of the total variation in a given trait is directly due to genetic differences between animals. The phenotypic identification of genetic superiority with respect to a given trait is subject to errors proportional in magnitude to the degree to which non-genetic sources of variation affect it. This formulation may be restated to read that the accuracy of selection of genotypes by phenotypic measurement of individuals is proportional to the *degree of heritability* of a character. Since only the hereditarily

determined fraction of the variation in any character will contribute to the improvement, the rate of change in the genetic composition of a population depends on that fraction as well as on the intensity of selection.

The degree of heritability is then the fraction of the total variance in a character which is due to genetic differences between individuals, or assuming additive gene action, the square of the correlation coefficient between the phenotype and the genotype (WRIGHT 1921). It may be best measured by considering the degree of resemblance observed between more and less closely related individuals, and several procedures for making such estimates have been developed by LUSH and his students (e.g. WHATLEY 1942). It should be obvious that different characters vary in this respect in different populations. For instance, in a group of animals highly inbred and closely related to each other, the degree of heritability of a given trait will be lower than in a random-bred population.

There are several means by which the breeder can increase the accuracy with which superior genotypes are identified. Thus a better estimate of the genotype of an animal can be obtained if information about the phenotypes of animals closely related to it is available. This in effect amounts to increasing the degree of heritability on an individual basis. The auxiliary information obtained from the sisters and brothers of a given animal (the sib test) or from its offspring (the progeny test) permits the breeder to increase the accuracy of selection.

The third factor which has been referred to as affecting the efficiency of selection is the interval between generations. It is clear that the annual rate of improvement depends on the number of years elapsing between successive generations. While there is a minimum interval which a breeder can not reduce (the period between conception and sexual maturity), he has considerable latitude in selecting younger or older animals for breeding purposes. The lower the average age of the parents of a given generation is, the less information the breeder has about them, and consequently the less accurate his selection. In the case of animals with a progeny test, the breeder is faced with a choice of using older animals about whose genotype he has considerable information, or the offspring of such animals whose genotypes are much less accurately known but who presumably originate from a generation already superior in its average genetic constitution to that of the progeny tested parents.

For larger animals, it has been shown by DICKERSON and HAZEL (1944) that the reduction in the age of parents will more than compensate for the advantage of the increase in accuracy of selection by progeny-testing, when the progeny test information is not available early in the animal's life, even when reproductive rates are relatively high and individual heritability low. Rather special conditions exist in the case of selection for egg production in the domestic fowl, so that an independent solution with respect to the most efficient balance between selection differentials, accuracy of selection and the interval between generations is called for. Accordingly, the purpose of this study is to determine which of several breeding schemes investigated will lead to the greatest rate of gain in the production index (hen-housed average).

The theory underlying the method by which such a determination can be made is rather complex and the computations involved extremely laborious. The details of the theoretical foundation are developed in the companion paper. The results to be presented here are merely solutions for several possible breeding schemes without a recapitulation of the statistical methods used.

THE UNIVERSITY OF CALIFORNIA PRODUCTION-BRED FLOCK

The basic data for the present study came from the production-bred flock maintained by the UNIVERSITY OF CALIFORNIA DIVISION OF POULTRY HUSBANDRY at Berkeley and selected for a high production index since 1933. The breeding methods used have been previously described in some detail by TAYLOR and LERNER (1938), and by LERNER and HAZEL (1947), so that only a résumé of the pertinent facts is necessary here. Each year in January an average of 11 sires and about 100 dams are selected for mating. Individually-pedigreed chicks are hatched in March and April in numbers sufficient to provide 400 to 700 pullets in the laying house at about five months of age. Lack of egg production during the hatching season, or of fertility or hatchability reduces the actual number of female parents to an average of 85. No comparable reduction is experienced in the case of the male parents because their reproductive performance is pre-tested before the hatching season, and only sires with reasonably high fertility are eventually used in breeding pens.

At the time that the following year's selection of breeders is made, the laying pullets are approximately nine months of age, and have been in production for about four months. Their production to this time (January 1) will be referred to as the part record, which can be considered as a partial progeny test for their parents, and a partial sister test for their sisters and brothers. Largely because of the fact that their own performance is known for only this short period of time the policy up to the present has been not to use these pullets for breeding in their first year of life. They are carried as an unculled population till the end of September of the year following the year of hatch, when the first laying year is considered to be terminated, and then subjected to selection for the following year's matings. Thus, all females (with occasional exceptions in the early years of selection) are two or more years old at the time chicks from them are produced.

The main basis of selection has been the sister test with the progeny test and individual selection also used to a certain extent. In the selection of individuals the primary criterion used in the past and at present is the number of eggs laid. The size of eggs and certain other characteristics of economic importance (egg quality, distribution of annual egg production) are also considered. The basis of family selection (sister and progeny tests), however, takes viability into account as well, so that the production of any individual or any group of birds is expressed in terms of the *production index:* the average number of eggs per original female housed. This measure is an approximation to a *total score* criterion, shown by HAZEL and LUSH (1942) to be a more efficient method of selection than that provided by independent culling levels for several desired characters.

FORMULATION OF THE PROBLEM

An analysis of the results obtained from 1933 to 1945 demonstrated that with respect to the production index, the genetic gains expected on the basis of known selection differentials, heritabilities, and inter-generation interval agreed very closely with the actual gains observed (LERNER and HAZEL 1947). The expected gains were computed for the three selection bases: individual performance, sister tests, and progeny tests. When the selection differentials for each of these were multiplied by respective heritabilities, and weighted for the respective proportions of the flock derived from parents selected on each of these bases, the expected genetic gain was found to be 10.25 eggs per generation. Since the average age of the parents was 1.94 years, this represents an expected gain of 5.3 eggs per year. The observed gain for the period studied was 5.6 eggs per year.

The fact that the observed gains agree with those expected indicates that the computations are based on valid assumptions. It is therefore possible to extend the computations to estimate the gains to be expected on the basis of preconceived selection schemes. The information necessary for such computations include:

1) Details of the selection scheme: numbers of birds of different ages selected out of the total number of birds of that age, and the basis of selection used for each kind of bird mated.

2) The number of offspring per dam. The value used in the present study was 7.06 daughters per dam at leg-banding time.

3) The standard deviation of the production index. On an individual basis this standard deviation was found to be 86.5 eggs for the full record, and 30.7 eggs for the part record in a sample of birds from the flock under study (this sample is described by LERNER and TAYLOR 1944).

4) The individual heritability of the annual production index (the full record). The estimate used in the present study was 0.05 found by LERNER and HAZEL (1947) to be approximately correct for the population studied.

5) The individual heritability of the production index to the end of December (the part record at the time selection for mating is made). The estimate used in the present study was 0.06 which is on the conservative side, since LERNER and CRUDEN (1948) have shown that the heritability of the part record (based on the production of survivors) is higher in the production-bred flock than the heritability of the full record. Furthermore, heritability estimates of the part-production index appear to be much higher in the sample of LERNER and TAYLOR (1944).

6) The genetic correlation between part and full record was found to be 0.75 by recomputing the data of LERNER and TAYLOR (1944). This is in rather close agreement with the genetic correlation of 0.74 found by LERNER and CRUDEN (1948) for survivors' production on the same basis.

7) Survival rates of females and males from maturity to one year of age, from one to two, from two to three and from three to four years of age. These were computed from the actual records extending over a period of several years. It should be noted that all but the first two of these rates were computed

for and applied to selected populations, and hence should not be taken as mortality tables for unselected flocks.

The companion paper demonstrates how these values enter into the formulae for determining the expected rates of improvement.

THE WEIGHTING OF SELECTION INDICES

It can be demonstrated both theoretically and from empirical data that family selection for egg production is more efficient than selection on the basis of individual records. In practice a combination of both methods is used, most breeders, however, being quite subjective with regard to the weights assigned to the family and to the individual. For the purposes of our computations, a more precise knowledge of the proper balance between the two criteria is needed. LUSH (1945) has shown that this balance depends primarily on the heritability of the trait selected for and on the size of family. The proper weighting can be readily computed for families of full sisters by solving for the multiple partial regression coefficients for family and individual records so as to maximize the correlations between the criterion of selection (a selection index -I) and the genotype of the individual. When the individual herself is excluded from the family average, the coefficient in the index is 0.27 for the dam and 0.73 for her sisters (averaging 6.06 in number). These coefficients are subject to but little fluctuation in the range of heritabilities from 0.04 to 0.07. The effect of changing the coefficient for the dam from 0.25 to 0.29 and for the family from 0.75 to 0.71 on the multiple correlation coefficient is only in the fourth decimal place. Hence, the computations were made on the justifiable assumption that the different types of selection practiced were based on the nearly optimum combination of family and individual records, which in the case under consideration assigns the individual record less than one-fifth of the weight of the family record.

THE BREEDING PLANS INVESTIGATED

Expected rates of gain were computed for several different schemes of female and male selection and the optimum combinations between them determined. With respect to the females, the plan designated as III in table 1 is essentially the plan currently used in the UNIVERSITY OF CALIFORNIA flock, and is widely practiced in the field. The first selection made is that of two-year old hens on the basis of the full records of themselves and their sisters. A year later, the second selection from the group thus chosen is made on the basis of the part records of their progeny. Finally, a third selection is made from the remainder at four years of age on the basis of the full records of the progeny.

Plans I and II advance this procedure by a year. Under both plans the first selection is made on the basis of individual and family records to January 1 of the first laying year. In plan I the pullets rejected are not further considered so that the second selection is made entirely from the birds chosen at one year of age. This selection is based on the full family and individual records. The third selection is similar to that under plan III, except that it occurs a year earlier.

Plan II is a variant of plan I in which the birds rejected on the basis of their part records are reconsidered at two years of age when they and their sisters have complete records. The third selection is applied to both groups of birds (2A and 2B in table 1). It should be noted that plan II at its extremes becomes identical with plan I on the one hand, and with plan III on the other.

TABLE 1

The bases of selection in the breeding plans investigated.

AGE IN YEARS	CLASS OF BIRDS	SELECTED FROM CLASS	BASIS OF SELECTION	PLANS FOR FEMALES			PLANS FOR MALES	
				I	II	III	L	M-R
1	1A	original flock	own record	part	part	—	—	—
			sisters' records	part	part	—	part	part
2	2A	1A	own record	full	full	—	—	—
			sisters' records	full	full	—	—	full
			progeny records	—	—	—	part	part
	2B	birds not used in 1A	own record	—	full	full	—	—
			sisters' records	—	full	full	—	—
3	3A	2A	progeny records	full	full	—	full	—
	3B	2B	progeny records	—	full	part	—	—
4	4	3A and 3B	progeny records	—	—	full	—	—

If no rejects are selected at two years of age it becomes plan I, whereas if no one-year old birds are used, it becomes plan III.

Plan L for the selection of males is identical with that practiced at present in the flock under study. As shown in table 1, the first selection is made at one year of age on the basis of the part records of sisters. At two years of age the second selection from these males is based on the part records of their progeny, and finally at three years of age the remainder are subjected to a further selection on the basis of the full records of the progeny. Occasionally a sire is used beyond three years, but for the sake of simplifying the computations such exceptional occurrences are not considered. The effect of this simplification is negligible so far as the results are concerned. Plans M to R utilize in the second selection the full records of the sisters as well as the part progeny records.

The numbers of birds used throughout are standardized to an average flock size of 600 pullets, and the number of breeding birds selected per year to the average used in the UNIVERSITY OF CALIFORNIA flock (85 dams and 11 sires).

A variety of age distributions is possible under each of the plans and a sufficient number of these were investigated to establish curves of expected gains for each of the plans for dams in combination with several variants of the basic plan for the sires. The latter are shown in table 2. As will be shown later

the most efficient of the plans for sires is the one designated P. Hence no plans involving a greater number of older sires than in plan L need investigating.

So far as the plans for the dams are concerned the age distributions investigated appear in the upper half of table 3. It should be noted that under plan II each of the sub-plans may have still further variants involving different ratios of 2A to 2B and 3A to 3B birds. The particular variants listed in table 3 were found by trial and error to be the optimum combinations for each sub-plan.

There is a rather important point in connection with the computed rates of gain per year in the production index which must be mentioned. Since ordinarily poultry breeders have to select for other characters in addition to the production index (such as egg size, egg quality, hatchability), the selection intensities for egg production possible are smaller than would be indicated by

TABLE 2

Distribution of sires under the different plans.

CLASS \ PLAN	L	M	P	Q	R
1A	5.9	8	9	10	11
2A	3.5	3	2	1	0
3A	1.6	0	0	0	0
Average age	1.609	1.273	1.182	1.091	1.000

the selection differentials computed on the basis of selecting the best 53, 61, 65 etc. of the pullets alive at the time that selection is made. The extent of reduction in the selection differential is variable and depends on the weight placed by the breeder on the other traits. In order to allow for this situation in the course of the computations 0.75 of the theoretical selection differential was used rather than all of it. This as will be shown below was too liberal a reduction. Hence, additional computations allowing the full selection differential to contribute to the gains were made for the best combinations under each plan.

RESULTS

The bottom half of table 3 shows the expected gains per year for each of the sub-plans in combination with the different schemes for the sires. The general trends are the same with all of the plans for the males, but it is clear that the maxima are obtained when plan P is used in combination with the various sub-plans for the dams. Apparently, the interrelations of the age of sires, the selection intensities, and the heritabilities are such that only twenty percent of the cockerels selected each year (two out of nine) should be repeated in the second year to achieve the maximum gains. The reduction in rate of gain due to an increased interval between generations incumbent on an increased number of older males is found to be greater than the additional improvement from the higher accuracy of selection.

TABLE 3

Distribution of dams by age and class and the gains per year expected under each plan in combination with the different plans for males.

PLAN		I						II					III				
AGE	CLASS	1	2	3	4	5	6	7–1	2	3	4	5	6–1	2	3	4	5
Distribution of the 85 dams by age and class																	
1	1A	53	61	65	69	77	81	85	77	69	65	61					
2	2A	22	19	16	14	7	4		7	12	15	16					
	2B								1	2	2	3	85	70	58.80	54.0	50
3	3A	10	5	4	2	1				2	3	4					
	3B											1		12	20.45	24.5	26
4	4													3	5.75	6.5	9
Average age of dams		1.494	1.341	1.282	1.212	1.106	1.047	1.000	1.094	1.212	1.271	1.341	2.000	2.212	2.376	2.441	2.518
Gain per year in number of eggs																	
	Plan L												3.96	4.06	4.03	4.00	3.94
	Plan M	5.45	5.72	5.71	5.76	5.78	5.76	5.69	5.78	5.75	5.72	5.65	4.17	4.27	4.23	4.18	4.12
	Plan P	5.53	5.82	5.80	5.86	5.89	5.86	5.80	5.88	5.85	5.82	5.74	4.20	4.30	4.26	4.21	4.15
	Plan Q	5.46	5.75	5.73	5.78	5.82	5.79	5.72	5.81	5.78	5.75	5.67	4.10	4.21	4.17	4.12	4.06
	Plan R	5.21	5.49	5.47	5.52	5.49	5.45	5.38	5.53	5.51	5.49	5.42	3.85	3.98	3.95	3.91	3.85

With respect to the results obtained within each plan for the dams definite trends may also be noted. Under plan I the optimum lies in the neighborhood of 90 percent as the proportion of pullets in the breeding flock. Reductions in gains ensue when this percentage is either decreased or increased. The situation is very similar to the one found with males. Under plan II the optimum once more is found in this general region, so that as a generalization it may be said that when yearling birds of either sex are being used for mating, a selection intensity of 10–20 percent on the basis of progeny testing leads to the most efficient gains.

Under plan III the situation is somewhat different. The optimum combination found is one in which a greater percentage of birds first used at two years of age are repeated in the following year. The age distribution used at present in the flock studied (plan III-3) is not far removed from the optimum. In a way this can be looked upon as a confirmation of the correctness of the theoretical basis of the computations. The present scheme is purely empirical and not rigid in any way. The selection intensities used vary from year to year depending on the results obtained and a reasonable degree of skill in selecting on this basis should on the average lead to an approximation of the theoretically optimum combinations, as it apparently does.

Further confirmation of the soundness of the theory on which the computations are based is found in the fact that when the expected gains are computed under the present plans for males and females (III-3 and L) without correction for reduced selection intensity they are found to be 5.37 eggs per year, a figure in remarkable agreement with the 5.3 eggs reported by LERNER and HAZEL (1947) and the 5.6 eggs actually realized. The reasons for the slight underestimate have already been given by LERNER and HAZEL, a further one appearing here in that the successful four-year old males not considered in these computations in all probability contributed additional gains.

If the same procedure of not reducing selection intensities is applied to the best of the plans I (I-5), II (II-2), and III (III-2), the range of the expected gains in combination with plan P for the males can be obtained. These upper limit figures are 7.83, 7.82 and 5.72 eggs for plans I-5, II-2 and III-2 respectively. It should be noted that even allowing the reduction to occur (some reduction must be allowed for, since in selecting pullets for mating less information on such characters as egg size and tendency to produce blood spots is available than for hens), plans I and II appear to be superior to plan III.

DISCUSSION

Thus it is clear from the data presented that plans I and II at their best lead to greater gains than any of the schemes under plan III. Although the latter may show higher rates of increase per generation they are more than offset by the shorter interval between generations incident on the use of pullets. In addition, considerable economies in breeding operation can be made under plan I and II, and especially so in the former. Instead of trapnesting all birds through the first laying year only the pullets mated and their full sisters need to be kept on traps after the first of January. The reason for continuing

to trapnest the sisters of breeding birds lies in the fact that the second selection is based to a considerable extent on family records. The rest of the flock should not be culled since annual flock means will aid in the establishment of less rigid and more efficient culling levels and will permit ascertainment of the progress being accomplished. For the breeder who bases his mating program on the consideration of the components of egg production, the procedure still permits the determination of the factors of viability, broodiness, and persistency even in the non-trapnested portion of his flock. The main objection to the use of pullets in the breeding flock lies in the fact that such pullets after producing offspring may die before the end of the first laying year, and presumably transmit this tendency to their progeny. Since the degree of heritability of first laying year survival is relatively low (LUSH, LAMOREUX and HAZEL 1946) this effect can not be very large, as already shown by the results presented. Furthermore, the possession of full records for this trait will enable the breeder to eliminate the descendants of undesirable families from the following year's flock.

In addition to the economic savings due to curtailment of trapping operations certain reproductive economies may be realized. Since pullets have a higher reproductive rate (egg production, fertility, and hatchability) a greater number of chicks per breeding bird will be obtained, thus permitting higher selection intensity. It should be noted that all of the computations were based on the assumption of an equal number of offspring from each bird. Since the pullets may be expected to produce a greater number of chicks in a given period of time than hens, the advantages ascribed here to the younger birds are actually underestimated.

With regard to progeny testing some explanation is necessary here. LERNER and HAZEL (1947) found that the offspring of tested parents have a higher production index than those of untested parents. Their results came from a flock where plan III was being used and indicated that progeny testing was an efficient way of improving production. As shown in table 3 all of the plans using some tested males (L to Q) are superior to plan III R where no tested males are used. However, under plans I and II the utility of progeny testing is greatly reduced, and the optimum percentage of tested parents in the breeding flock is lower than under plan III. This is due to the fact that while the use of part-progeny records advances the age of parents by 50 percent (from two to three years of age) under plan III, under plans I and II this advance is a full 100 percent (from one to two years of age). Hence, progeny testing must be considered a valuable aid only when no pullets are used in the breeding flock. Where the optimum percentage of pullets in the breeding flock is 90, the optimum percentage of part-tested males is not more than 20. Their use increases the gain expected when 100 percent of the breeding males are cockerels by only seven percent.

The question of sister testing, however, must be answered in an entirely different light. Some intensity of selection on individual performance is sacrificed when selection is based on family records, but in proportion less than the

effect of increased accuracy of selection. Furthermore, family selection does not increase the interval between generations. In the computations leading to the establishment of the curves of genetic gain for the various plans, it was shown that the weighting of the family record (excluding the dam) to the individual record with an average family size of 7.06 is 0.73 to 0.27. If the family average includes the individual the weighting becomes about 5.8 to one. Experimental data are presently under analysis to validate these theoretical ratios. It is clear, however, that sister testing is indispensable in an efficient breeding plan and is basic to any variation of the plans studied and, most likely, to any other plans which can be devised. *In fact, the conclusions derived are applicable only to schemes based on family selection.*

The last question which may be considered is with regard to the universality of application of our findings. It is possible to argue that the results obtained apply only to the particular flock under consideration. It is, however, quite apparent that while the exact optima may apply specifically only to this particular flock, the general principles established here are valid for a wide range of cases. If the theory upon which the computations are based is correct (and that is verified by the close agreement between it and the actual results obtained here and in the analysis of, LERNER and HAZEL, 1947), the only questions that may be raised are with respect to the universality of the statistical constants employed in the computations. Wide variations in the four basic constants used are possible without affecting the general trend of the results. There is good evidence, moreover, that most flocks with like production characteristics have not too dissimilar standard deviations of the production index, heritabilities of part and full records, and genetic correlations between them. Since exact statistics for other flocks have not been published this assertion is not directly verifiable. However, similar data for the production of survivors of this flock can be compared with the data reported for other strains and breeds, and as it may be seen from the report of LERNER and CRUDEN (1948) they fall into the same general range. It may then be concluded with a reasonable degree of confidence that the consequences of the findings in this study can be widely applied. It should be noted, however, that computations have been made for only one family size (7.06) daughters. On the other hand, it should be emphasized that the conclusions reached are based on conservative estimates of plans I and II. The allowance made for the damping of selection differentials is probably too high, as judged by the comparison of the gains under plan III as computed (with the 0.75 correction factor) and as actually realized. Even more important in this connection is the fact that all of the computations envisage a rigid flock structure without deviation from year to year. Exercise of proper judgment in selection, so that the actual number of repeated males and females would vary depending on the results obtained, would permit greater gains than computed.

SUMMARY

An investigation of the expected rates of gain in the production index under various age distributions of the breeding flock reveals that greater efficiency is

obtained by a more widespread use of younger birds. The optimum plan investigated is one in which 90 percent of the breeding flock consists of pullets and 10 percent of two-year old hens selected on the basis of their sisters' and daughters' records. Similarly, about 80 percent of the breeding males used each year should be cockerels. Under this scheme the utility of the progeny test is considerably reduced, because its use doubles the interval between generations in the case of each bird so selected. Where two-year old birds are mated for the first time, the progeny test has considerable value since in this case the interval between generations is for each bird increased by only 50 rather than by 100 percent. The above conclusions apply only to cases where the primary criterion of selection is the family record and the individual record is of relatively minor importance. The use of the breeding plans involving a high percentage of pullets not only leads to more rapid improvement but also results in a considerable saving in the cost of breeding operations.

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THE OPTIMUM STRUCTURE OF BREEDING FLOCKS. II. METHODS OF DETERMINATION

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THE preceding paper by DEMPSTER and LERNER has presented the results obtained in the determination of expected genetic gains in egg production under different age compositions of a breeding flock. In it the theoretical and practical consequences of following a given breeding plan were emphasized but the statistical model on which the computations were based was not presented. The purpose of this report is to describe such a model and to demonstrate the methods used in computing the expected gains. They are essentially

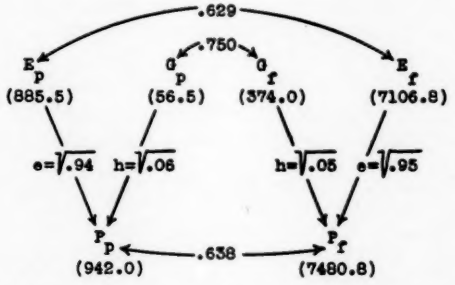


FIGURE 1.—Characteristics of flock underlying all calculations of gains. For explanation of symbols see table 1. The figures in parentheses represent variances. Single-headed arrows represent paths and double-headed arrows correlations. (WRIGHT 1921.)

an extension of the work of DICKERSON and HAZEL (1944), and are based on path relationships first established by WRIGHT (1921).

The companion paper described the data and the sources from which they were taken. The meaning of the symbols used throughout is presented in table 1, while figure 1 shows the statistical constants on which the computations are founded. The fundamental postulate involved is that the effects of genetic and environmental differences on egg production are strictly additive and determine the phenotypic values completely ($h^2+e^2=1$). The justification of this postulate lies in the fact that it is chiefly the additive effects of gene differences for which the methods of selection employed are effective, and that it is chiefly the additive effects which contribute to the computed values of the correlation (h) between genotype and phenotype. The non-additive interactions of genetic and environmental differences are then included in the computed values of the correlation (e) between environment and phenotype. There is considerable concord that this model constitutes a useful and workable

TABLE 1

	SYMBOL	EXPLANATION OF SYMBOLS
1	a	Path coefficients.
2	b	The value of the abscissa at the point of truncation of a normal curve.
3	h	Path coefficient from genotype to phenotype. Heritability (h^2) is the fraction of the total variance attributable to additive genetic differences.
4	D	The subscript indicating that the symbol refers to a dam or a prosepctive dam.
5	E	The combination of environmental and non-additive genetic effects.
6	e	Path coefficient from environment to phenotype, including non-additive genetic and environmental interactions.
7	f	The subscript indicating the full record (average production from beginning of lay to September 30 of the following year per bird housed).
8	G	The genotype (average additive effects of genes). The subscripts 1, 2, 3 refer to the genetic components of the corresponding selection indices.
9	ΔG	Change in average value of genotypes due to selection. The subscript g refers to the gain per generation; the subscript y to the gain per year.
10	GC	The portion of the genetic contribution from parents that is independent for each member of the progeny of given parents. The mean value of GC is zero and the mean contribution of GC to variance both within families and between individuals of different families is one-half the total genetic variance in random bred populations in equilibrium. Generally used as a subscript to σ.
11	GD	The portion of the genetic contribution from a dam that can be considered constant for all her offspring. The value of GD is one-half the value G of the dam and the contribution of GD to genetic variance within families is zero. The contribution of GD to genetic variance between individuals of different families is one-quarter the variance of G of the dams ($=\sigma_{GD}^2/4$)
12	GS	The same as GD but contributed from sires instead of dams.
13	I	Average superiority of the selected group over the original population in terms of standard deviations.
14	I	The selection index combining the record of the individual and of relatives. I_1 is equal to the sum of the products (.27 times the part record of a bird) and (.73 times the average part record of her sisters); I_2 is the second index similarly based on the full instead of part records; I_3, the third index, is the average part record and I_4 the average full record of the progeny.
15	n	The original number of females housed per full-sister family.
16	p	The subscript indicating the part record (average production from beginning of lay to September 30 of the following year per bird housed).
17	P	The phenotypic value expressed in eggs laid in the period indicated by the subscript.
18	r	Product-moment or intra-class correlation coefficient.
19	S	The subscript indicating that the symbol refers to a sire or a prospective sire.
20	w	The weighting factor entering an index. The subscript A refers to the mean records of the sisters of a dam or prospective dam; the subscript D refers to the record of the dam or prospective dam herself.
21	σ	Standard deviation of the variable indicated by subscript.

approximation (WRIGHT 1935; LUSH 1945), and agreement between computed and observed rates of gain in at least one poultry flock offers adequate confirmation of this viewpoint (LERNER and HAZEL 1947).

THE BASIS OF SELECTION

Following DICKERSON and HAZEL (1944), it is clear that the gain in genetic merit per generation (ΔG_g) obtained by selecting a given proportion of the

birds on the basis of their full-record phenotype is ī h, where ī is the average superiority of the selected group over the whole population in terms of standard deviations. The values of ī can be obtained either from PEARSON'S Tables (1931) or computed for small populations from the ranked ordinate values tabulated by FISHER and YATES (1938). The values of ī given in these tables are for sharply truncated populations where selection is practiced for only one character. If, as is usually the case, allowance is to be made for selection for other characters, the value of ī must be reduced to some extent. As already noted in the preceding paper the factor 0.75 was used in our computations for this purpose.

When selection is made on the basis of the part rather than of the full record the value ī h must be further mulitplied by the genetic correlation between full and part record ($r_{G_f G_p}$) to obtain the estimate of genetic gain in the full record. To convert the computed gains into terms of eggs the appropriate values of standard deviations of genotypes ($h\sigma_f$) must be further introduced into the formula for ΔG_g.

More accurate selection, and hence greater gains, can be made by using a selection index rather than the bird's own record. In the case of the sires the use of such an index is mandatory, since no phenotypic expression for males is available for egg production. The index may be based on the records of the relatives of a bird (sisters or daughters) and the respective weights assigned to the bird's own record and to that of its relatives so as to maximize the correlation between the index used and the bird's genotype (r_{IG_f}). The expected gains under this method of selection can be computed in a fashion analogous to the one used in selection on the basis of individual records, except that instead of the correlation between phenotype and genotype, the correlation used here is that between the index and the genotype.

GENETIC VARIANCE

In poultry, contrary to the case of multiparous mammals, the environmental contributions to the total variance may be considered with but little error to be independent for each individual. The genetic variance in a random-bred flock at equilibrium consists of three fractions: (1) one quarter due to those contributions of the sires that are constant for all the offspring of a given sire, (2) another quarter due to those contributions of the dam that are constant for all the offspring of a given dam (3) one-half due to chance at segregation. If, however, the sires and dams are selected samples, rather than random representatives of their generation, the relative values of these three components are altered.

The first two components are clearly proportional to the genetic variances of the parents since, as far as additive gene differences are concerned, the genotypic expectancy of offspring is the mean genotypic value of their parents. Calculation of these portions of the variance, when applied to the whole group of parents used in a given year, must take into account both the mean genotypic values of the sires and dams of each age group and the variance of each group around its mean. The determination of the resulting total parental genotypic variance for any particular system of mating depends, therefore,

on rather extensive iterative calculations. Sample calculations have indicated an overall reduction in parental genotypic variance of approximately four percent and inasmuch as the exact value is not at all critical this figure has been used for all the mating schemes. Wherever a group of individuals of given age are progeny tested, however, the exact reduction in genotypic variance to be expected for the group under consideration has been computed and used.

The third component of variance, due to chance at segregation, is a function of the heterozygosity of the parents. This component in the offspring of selected parents is not, in the absence of additional postulates, subject to calculation. The actual change in this component may be reduced, remain constant, or be increased in a population mating at random (except that selection is being practiced), depending upon the exact gene frequency distribution at any given time. In the present calculations, we have postulated that the chance component would be increased sufficiently to compensate for the decrease in the constant components from the selected sires and dams. There are several reasons for adopting this postulate. Firstly, experience has shown that the heritability of economic characters decreases rather slowly under selection, and that at least a part of such decrease can be accounted for by inbreeding. Secondly, where genetic variability is due to a large number of gene differences, the total genetic variation is changed very little by selection (LUSH 1945). Finally, this postulate permits the assumption of a constant gain per generation which greatly facilitates the necessary computations. In the calculations, therefore, the constant contributions for sires and dams are each taken as 24 percent of the total genetic variance and the chance component is taken as 52 percent, instead of the 25, 25 and 50 percent which would have been correct if no selection of the parents had been practiced.

The actual variances used in the computations were as follows:

CHARACTER	VARIANCE DUE TO CONSTANT CONTRIBUTIONS FROM SIRE	VARIANCE DUE TO CONSTANT CONTRIBUTIONS FROM DAM	VARIANCE DUE TO CHANCE AT SEGREGATION	TOTAL GENETIC VARIANCE
Part record	54.2/4	54.2/4	58.8/2	56.5
Full record	359/4	359/4	389/4	374

SELECTION ON THE BASIS OF I_1

We may first consider the problem of selection of dams from the unselected flock on the basis of index I_1 which is a weighted average of the prospective dam's own record to January 1 of her first year of life and the mean record of her full sisters to the same date. In order to obtain the optimum weighting and the multiple correlation between the index and the prospective dam's genotype for part record by ordinary multiple correlation methods, the following information is necessary:

(1) The correlation between the prospective dam's genotype and her record, which is simply the square root of the heritability ($\sqrt{.06} = .2449$).

(2) The correlation between records of sisters: this is equal to heritability multiplied by genetic correlation. Since the genotypes of sisters are correlated only through the constant contributions of their parents, the genetic correlation is equal to the proportion that this constant contribution to variance is of the total contribution to variance, or (taking the values from the table given above)

$$\frac{54.2/2}{56.5} = .480.$$

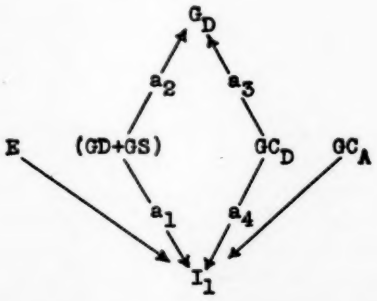
Multiplying this by the heritability (.06) we obtain .0288, the correlation between part records of sisters.

(3) The correlation between the prospective dam's genotype and the record of a sister, which is equal to the correlation between sisters' genotypes multiplied by the correlation between a bird's genotype and her record or (.480) $\sqrt{.06} = .1174$.

(4) The number of sisters including the dam, which is taken here as 7.06, the mean value for the flock.

The multiple correlation turns out to be .353 and the relative weighting of dams' records and the average of the records of the dams' sisters are .28 and .72 respectively. The optimum weighting can also be obtained by substituting the appropriate values in the formula of LUSH (1945, p. 321), where n = 7.06, r (genetic correlation between sisters) = .480 and t (phenotypic correlation between sisters) = .0288. An algebraic adjustment is necessary in order to obtain the weighting of the family of sisters excluding the dam. The result is identical with that obtained by the method described above.

If the weighting factors entering into index I_1 (w_A for mean value of sisters and w_D for prospective dam) are not optimum, the correlation between index and dam's genotype for part record may be easily computed on the basis of the following path coefficient diagram:



The correlation is $(a_1a_2)+(a_3a_4)$ where the a's are the path coefficients indicated in the figure. Since G_D is the sum of the independent values (GD+GS) and GC, the path coefficients a_2 and a_3 are respectively equal to

$$\frac{\sigma_{GD+GS}}{\sigma_{G_D}} \text{ and } \frac{\sigma_{GC}}{\sigma_{G_D}}, \text{ or } \frac{\sqrt{54.2/2}}{\sqrt{56.5}} \text{ and } \frac{\sqrt{58.8/2}}{\sqrt{56.5}}$$

I_1 is equal to the following:

$$\frac{w_A}{n-1}\left[\sum_{1}^{n-1}(E + GC_A)\right] + (GD + GS) + w_D(GC_D + E)$$

and the standard deviation of index I_1, is therefore equal to:

$$\sqrt{\frac{w_A^2}{n-1}(\sigma_E^2 + \sigma_{GC}^2) + \sigma_{GD+GS}^2 + w_D^2(\sigma_{GC}^2 + \sigma_E^2)}$$

$$= \sqrt{\frac{w_A^2}{6.06}\left(885 + \frac{58.8}{2}\right) + \frac{54.2}{2} + w_D^2\left(\frac{58.8}{2} + 885\right)}$$

The path coefficient a_1 is then equal to:

$$\frac{\sigma_{GD+GS}}{\sigma_{I_1}}\left(=\frac{\sqrt{54.2/2}}{\sigma_{I_1}}\right),$$

while a_4 is equal to

$$\frac{w_D\sigma_{GC}}{\sigma_{I_1}}\left(=\frac{w_D\sqrt{58.8/2}}{\sigma_{I_1}}\right).$$

Following this method the multiple correlations obtained for different weightings were:

w_A	w_D	MULTIPLE CORRELATION BETWEEN I_1 AND G_{D_p}	NOTES
.77	.23	.351	Over-weighting of family average
.72	.28	.353	Optimum weighting
.67	.33	.351	Over-weighting of individual record

The value obtained for optimum weighting is of course identical with that given by the ordinary multiple correlation methods. The effect of over- or under-weighting the dam by five percent reduced the multiple correlation by just a little more than one-half of a percent of its maximum value. It may thus be seen that the exact weightings are not at all critical. Furthermore, calculations for different values of genetic and environmental correlations occurring among selected or unselected parents in the cases considered indicate that the optimum weightings themselves will not differ very much from the values computed above. The use of a constant weighting for unselected one and two year old birds whether or not they were subjected to previous selection simplifies the problem of the practical breeder and also reduces the labor in the calculation of correlations between index and genotype under repeated selec-

tion. For these reasons the calculated gains have been based on a constant weighting for indices I_1 and I_2. The values chosen as most suitable for all the cases considered are: $W_A = .73$, $W_D = .27$. Under these conditions the correlation $r_{I_1 G_{D_p}}$ is .353. This figure, multiplied by the genetic correlation between part and full record, gives the value .265 for the correlation between I_1 and the genotype for full record. In turn .265 is multiplied by $\bar{i}$ (the average superiority of the index I_1 of the selected animals obtained as described previously) to yield the average gain in genotype for the full record.

SELECTION ON THE BASIS OF I_2

The previous section dealt with selection from an unrestricted population on the basis of an index for part records. This is the first selection under plans I and II described in the companion paper. The first selection under plan III is based on a similar procedure, the correlation between I_2 and the dam's

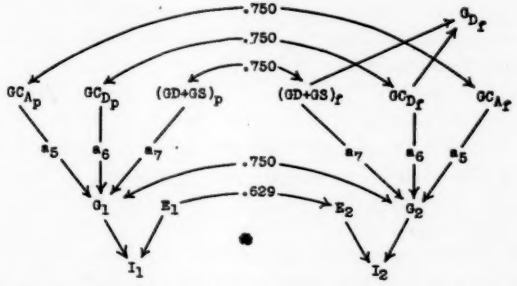


FIGURE 2.—Relationships between I_1, I_2 and G_{D_f}. For explanation of symbols see text.

genotype for the full record being calculated in the same manner as the correlation between I_1 and the dam's genotype for the part record. However, in the case of the second selection under plans I and II the situation is altered.

The fundamental difference here lies in the fact that, due to the first selection, the correlations previously determined are no longer valid. In particular, it may be expected that the genetic and environmental components of I_1, as well as of I_2, have become negatively correlated among the once selected animals, because animals with a low environmental component would have been retained only if their genetic component were high, while those with a low genetic component only if their environmental component were high. The gains to be expected depend, for a given correlation between the two indices, on the way in which this correlation is partitioned into its environmental and genetic components. The following discussion is based on the postulate that the distributions, among a group of birds already subjected to selection, of indices I_2, I_3, and I_4 and their genetic and environmental components retain the characteristics of random samples of normal distributions. This postulate is not strictly correct although the errors due to it, as in the similar cases discussed by DICKERSON and HAZEL (1944), are likely to be small.

In the text figure in the previous section, I_1 was shown as the sum of four independent components, three of which were genetic and one environmental. Figure 2 shows the same breakdown for both I_1 and I_2, but with the sum of the three genetic components shown separately as G_1 and G_2 for the two indices. It should be noted that the paths indicated as a_5, a_6, and a_7, are the same for both indices because the weightings of the dam and the sisters are the same for both indices and also because the relative values of the three genetic components are postulated to be the same. The correlation between each of the three genetic components for the part index and the corresponding component for the full index among unselected birds is the genetic correlation of .750 since their respective variances are, in a sense, random samples of the total genetic variance. The correlation $r_{G_1\ G_2}$, then also becomes .750 since $a^2_5+a^2_6+a^2_7=1$.

It is important to note that the correlation between G_1 and any of the components of G_2 is the same irrespective of the paths through which it is traced. Thus $r_{G_1GC_{D_f}}$ is the same whether the route $G_1-GC_{D_p}-GC_{D_f}$ or the route $G_1-G_2-GC_{D_f}$ is taken. Hence it is legitimate to consider that selection on the basis of I_1 affects the components of G_2 and the dam's genotype for the full record solely through its effect on G_2.

The first step in computing the correlation between I_2 and G_{D_f} among the previously selected animals is to compute the variances of E_2, G_2, and I_2 in this group. The reduction in these variances is related to the reduction in the variance of I_1. The variance of I_1 of the restricted group is, in turn, related to that of the original group as the variance of the selected tail of the normal distribution is to that of the whole distribution. The proportional reduction in variance is $\bar{\imath}$ ($\bar{\imath}$-b), where b is the abscissa at the point of truncation (DICKERSON and HAZEL 1944). If it is postulated that the portion of the variance of a dependent variable not accounted for by its regression on the independent variable is independent of the latter, the proportional decrease in the variances of the dependent variables E_2, G_2, and I_2 can be readily obtained, since it equals the proportional decrease in the independent variable multiplied by the square of the correlation between the dependent and independent variables, a relationship also used by DICKERSON and HAZEL (1944).

With the variances of E_2, G_2, and I_2 of the selected animals thus determined, the new path coefficients and correlations can be computed. Since I_2 is the sum of E_2 and G_2, the path coefficients to I_2 from each of the others are the respective square roots of the ratios of their variances. The variance of I_2 can be set equal to the sum of $\sigma_{E_2}^2$ and $\sigma_{G_2}^2$ plus twice the product $\sigma_{E_2}\sigma_{G_2}r_{E_2G_2}$. From this relationship the new $r_{E_2G_2}$ may be computed, as illustrated in figure 3 for a specific selection intensity (plan I-5 of the preceding paper). The correlation between I_2 and G_2 is equal to the sum of the direct path plus the product of the path from E_2 to I_2 and $r_{E_2G_2}$. In the case illustrated the correlation has been reduced from .40 to .303 as a consequence of the first selection.

It has been pointed out that the effect of selection on the basis of I_1 on the prospective dam's genotype can be considered as operating through its effect on G_2. Selection on the basis of I_2 likewise operates through G_2. We may then utilize the principle that restriction of an independent variable (in this case

G_2) does not alter the concrete regression coefficient of a dependent variable on it. The regression of the prospective dam's genotype on G_2 is then the same in the selected group as among all the animals. The correlation is, however, reduced, and this reduction may be computed in terms of the constant regression and the new variances, if desired. The results of such a computation are also shown in figure 3.

In plan II selection is also made among two-year old birds that were rejected in the first selection made on one-year old birds. The procedure here is exactly

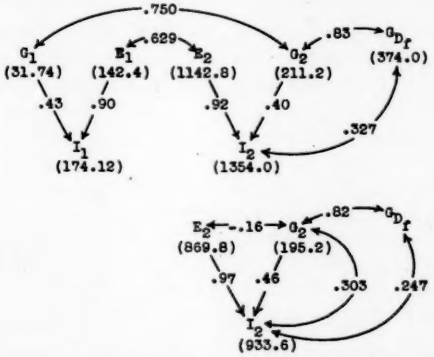


FIGURE 3.—The effect of selection for I_1 on I_2. The upper path diagram represents the relationships before selection; the lower diagram shows the reduced variances and altered correlations after the original population has been subjected to the first selection under plan I-5. Note the negative correlation between E_2 and G_2 (−.16) as against independence in the original population, and the reduction in $R_{I_2}G_{D_f}$ from .327 to .247.

parallel to that described above, due account being taken of the negative gain made in the first selection.

SELECTION ON THE BASIS OF I_4 UNDER PLANS I AND II

The next selection in plans I and II is that based on index I_4, so that it may be considered before index I_3. The correlation needed to compute the gains from the selection on the basis of progeny records is that between the dam's genotype and the average of her daughters' full records. Since each daughter is provided with a new environment independent of the previous selection processes, the computation of this correlation presents no difficulties. The variance of I_4, which is the average of the 7.06 daughters in a family, is equal to

$$\sigma_{GD}^2 + \sigma_{GS}^2 + \sigma_{GC}^2/7.06 + \sigma_E^2/7.06.$$

The first term in this expression is a quarter of the genetic variance remaining in the dams after the first two selections and is computed for each selection plan. The second term, σ_{GS}^2, is $54.2/4$ since each dam has an equal chance of being mated to any sire. This and the other terms are mutually independent.

The correlation coefficient between the dam's genotype and I_4 is the square root of the fraction that $\sigma_{GD}^2/4$ forms of the total variance of I_4. Applying the correlation thus obtained to the constants appropriate to the given selection intensities, ΔG_g may be obtained for this index in the same fashion as the previous ΔG_g's.

SELECTION ON THE BASIS OF I_3

The computations for plan III are similar in theory to those already described. The first selection is made at two years of age on the basis of the full records of the bird and of her sisters. For the second selection the proportional reduction in the variance of the dams' genotypes for the part record is required. That for the full record may be computed in the manner already described and is converted into the reduction in variance for the part record by multiplying it by $(.750)^2$, .750 being the genetic correlation between the part and the full record. Assuming a constant regression coefficient the new genetic correlation is found to fall between .730 and .733 for the various subplans of plan III. Knowing this value, it is possible to compute the correlation between I_3 (average part records of the daughters) and the dam's genotype for the full record along the path leading through the genetic components of I_3 and the dam's genotype for the part record to the dam's genotype for the full record.

SELECTION ON THE BASIS OF I_4 UNDER PLAN III

Third selection under plan III is based on the average full record of the daughters (I_4). The determination of gains requires a knowledge of the new correlations existing between I_4 and its genotypic components and between them and the genotype of the dam for the full record. The computation of these correlations is rather involved if account is taken of the differences in the correlations between values of the genetic components for the full and the part records. The genetic correlation for the component due to chance at segregation is .750, for the component due to constant contributions of the dam to all her offspring lies between .730 and .733 for the various subplans of III, and the compoment due to constant contributions of the sire is slightly less than .750 depending on the particular breeding scheme used. Inasmuch as the differences are very small, computations were made on the postulate that all the genetic correlations were of the magnitude of the lower of these three values, namely, the value computed for the constant contributions of the dam. This postulate greatly simplifies the calculation of the correlation between I_4 and the dam's full genotype. The procedure is very similar to that described above for index I_2, the first step being the determination of the negative correlation between genetic and environmental components of I_4.

SELECTION OF SIRES

The determination of the gains from sire selection is similar to that described for the dams but somewhat simpler because the sire himself has no production record. However, since the number of sires selected is smaller than the number of dams, while their contribution to the heredity of the daughters is fully as

great, it is worthwhile to base the second selection on a combination of indices I_2 (the average of daughters' part records) and I_2 (the average of the full records of sisters). The method by which the gains due to selection on the basis of the combined index are computed is illustrated in figure 4.

The computation of the correlations with respect to index I_2, which are

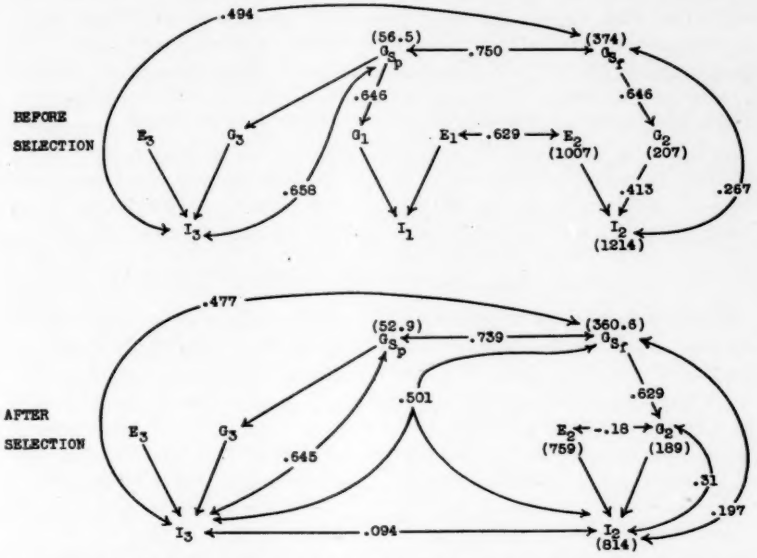


FIGURE 4.—The selection of sires. The upper path diagram shows the relationships between I_1, I_2, I_3 and G_{Sf} in the original unselected population. The lower diagram shows the reduced variances and altered correlations after the original population has been subjected to the first selection under plan P. Note the correlation of .477 between G_{Sf} and I_3 which is about 95 percent of the multiple correlation of .501 between G_{Sf} and the optimum combination of I_2 and I_3.

altered as a result of the previous selection on the basis I_1, needs no further comment since it is similar to that already described for the dams. The method for computing the reduced value of the genetic correlation between the full and the part records has also been given. Since GS of the offspring equals one-half of G_S of the sire, the square of the correlation between I_3 and the sire's genotype for the part record, in the case of a sire mated to 7.73 dams each having on the average 7.06 daughters, is the proportion that one quarter of σ_{GSp}^2 is of the variance of the daughters' average, namely:

$$\frac{\sigma_{GSp}^2/4}{\sigma_{GSp}^2/4+54.2/(4\times7.73)+58.8/(2\times7.73\times7.06)+885.5/(7.73\times7.06)}.$$

The value of σ_{GSp}^2 to be used in this formula is computed separately for each mating plan.

Indices I_2 and I_3 are themselves correlated, but only through their separate correlations with the sire's full genotype. The product of these correlations therefore yields the correlation between the two indices. Their combination into a single index is a simple problem in multiple correlation. From figure 4 it is evident that the part records of the sire's daughters give much more information than the full records of his sisters. This is because of the large number of offspring, the fact that each sire is mated to several dams whose average contribution to the variance of I_3 is small, and the previous use of the sires' sisters in the first selection. In the case considered only about five percent of the gain is due to the addition of information from the sire's sisters. It should be understood that what is termed selection of sires here, is actually selection of full sister families, only one brother being used from each family selected. Computed gains would be greater if all the males selected were from the best family, but it is thought that the consequent effects of increased inbreeding would interfere with the realization of computed gains.

COMPUTATION OF THE ANNUAL RATES OF GAIN

DICKERSON and HAZEL (1944) have shown that the expected genetic gain per year (ΔG_y) may be computed by adding the ΔG_g's weighted for the proportions of the total group of breeding animals which each selected group forms (assuming equal number of offspring per parent from each group), and dividing the sum by the average age of the parents. Table 3 of the preceding paper shows the values of ΔG_y for the various plans of dam selection combined with the various plans of sire selection. The mechanics of these computations are rather simple and may be illustrated by the figures pertaining to plan I-5 in combination with sire plan P.

The gain expected from the first selection of 77 dams out of 510 females alive at one year of age was found to be 5.966/2; from the second and third selections out of the latter group 5.887/2 and 4.302/2. The divisor 2 is used because only one-half of the gain from each parent is realized in the offspring. It cancels out in the formula for ΔG_y appearing below. The appropriately weighted summation of these figures is

$$[77(5.966) + 7(5.966 + 5.887) + 1(5.966 + 5.887 + 4.302)]/(2 \times 85)$$

which equals 6.572/2 eggs. Similar computations for the sires indicate a gain of 6.902/2 eggs. The average age of the dams in this scheme is 1.106 years, while that of the sires is 1.182 years. Hence,

$$\Delta G_y = \frac{6.572 + 6.902}{1.106 + 1.182} = 5.89 \text{ eggs per year.}$$

The other values recorded in table 3 of the companion paper have been obtained in an identical fashion.

SUMMARY

A method of computing the expected genetic gains on the basis of specified

selection plans is presented as applied to the problem of breeding for high egg production.

ACKNOWLEDGEMENT

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THE PRODUCT METHOD OF CALCULATING LINKAGE FROM F_2 DATA INVOLVING SEMISTERILITY; AND ITS APPLICATION TO A BARLEY TRANSLOCATION[1]

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INTRODUCTION

IN CORN linkage studies with semisterility due to chromosomal interchange between non-homologues have been based largely on backcross data. In a plant such as barley, backcrosses are not feasible. Since semisterility in F_2 populations behaves differently from any other character, special formulae are necessary for calculating linkage intensities. This paper presents formulae for the application of the product method to such F_2 data. Linkage studies with a chromosomal translocation in barley are also reported.

Linkage data with the first case of semisterility in the Florida velvet bean, *Stizolobium deeringianum* Hort. were reported by BELLING (1915). WELLENSIEK and KEIJSER (1929) reported linkages with a dominant *Q* factor for aborted ovules in Pisum, but the character segregated in a 3:1 ratio; and no information was available on its cytology. PELLEW (1940) reported linkages based on F_2 data with translocations in Pisum, but the methods used in the calculation were not presented. HONECKER (1936, quoted by KATTERMANN 1939) observed the different types of sterility in barley but all types except the trisomics showed seven bivalents and therefore probably were not due to chromosomal interchange. LUTHER SMITH (1941) reported an inversion and two reciprocal translocations in addition to trisomics and a tetraploid in barley. The analysis of F_3 linkage data in barley and the combination of F_2 with F_3 data using the "maximum likelihood" method were reported by IMMER and HENDERSON (1943).

THEORETICAL F_2 RATIOS AND FORMULAE FOR CALCULATING LINKAGE INTENSITY

In cases where F_2 data are utilized for linkage tests, the theoretical ratios to be expected with different amounts of crossing over between two Mende-

[1] Contribution from the DIVISION OF AGRONOMY AND PLANT GENETICS, UNIVERSITY OF MINNESOTA, St. Paul, Minn. Paper No. 2357, Scientific Journal Series, MINNESOTA AGRICULTURAL EXPERIMENT STATION. Part of a thesis presented in partial fulfillment of the requirements for an M.S. degree.

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lian character pairs may be calculated according to the general method set up by IMMER (1930) and earlier by FISHER and BALMUKAND (1928). The formulae for F_2 and F_3, together with the method of their derivation, have been summarized recently by KRAMER and BURNHAM (1947). In an F_2 linkage test involving a simply inherited character pair (Aa) and semisterility due to chromosomal interchange vs. normal (designated *Bb*) the Aa pair will segregate in a 3:1 ratio, while the *Bb* pair will segregate in a special 1:1 ratio of semisteriles (*Bb*) to normals, the normals being of two equally frequent types either standard (*bb*) or homozygous interchange (*BB*) normals. Special formulae and tables are necessary for applying the product method to the calculation of linkage and for determining standard errors from such data.

Assuming no difference in crossing over between the two sexes, p being the recombination value in repulsion, the four classes of male and female gametes for repulsion (where semisterility entered the cross with the *aa* parent) will be:

$$\underset{\frac{p}{2}}{AB} \qquad \underset{\frac{1-p}{2}}{Ab} \qquad \underset{\frac{1-p}{2}}{aB} \qquad \underset{\frac{p}{2}}{ab},$$

and the frequencies of the F_2 genotypes within each F_2 phenotype are as follows:[1]

A PHENOTYPES				*a* PHENOTYPES			
SEMISTERILES (a)[2]		NORMALS (b)[2]		SEMISTERILES (c)[2]		NORMALS (d)[2]	
		Standard:				Standard:	
$(2p-2p^2)$	*AABb*	$(1-p)^2$	*AAbb*	$(2p-2p^2)$	*aaBb*	p^2	*aabb*
$(2-4p+4p^2)$	*AaBb*	$(2p-2p^2)$	*Aabb*				
		Homozygous Interchange:				Homozygous Interchange:	
		p^2	*AABB*			$(1-p)^2$	*aaBB*
		$(2p-2p^2)$	*AaBB*				
Totals $(2-2p+2p^2)$		$(1+2p-2p^2)$		$(2p-2p^2)$		$(1-2p+2p^2)$	

For the totals in the four phenotypic classes and for the genotypic frequencies except those which are completely homozygous (*AAbb*, *AABB*, *aaBB*, and *aabb*) the actual formula remains the same for coupling after substituting $(1\text{-}p)$ for p in the repulsion formulae.[3] For the completely homozygous genotypes (*AAbb*, *AABB*, *aaBB*, and *aabb*) the formulae are different for coupling

[1] For ease in setting up these formulae the "4" in the denominator of each expression has been dropped. If used in determining the expected frequency in any class or genotype of a given population, the "4" in the denominator should be restored.

[2] These letters: a, b, c, d, indicate the four phenotypic classes in F_2 (table 1).

[3] For example the substitution of $p=.10$ representing ten percent crossing over in repulsion gives the same result as does the substitution of $p=.90$ representing ten percent crossing over in coupling.

TABLE 1

Expected percentage frequencies in F_2 corresponding to different crossover values between a simply inherited character pair Aa and semisterility—coupling or repulsion phase.

PERCENT CROSSING OVER	PHENOTYPIC CLASSES			
	a *A* SEMISTERILE	b *A* NORMAL	c *a* SEMISTERILE	d *a* NORMAL
0.00	50.000	25.000	0.000	25.000
0.01	49.505	25.495	0.495	24.505
0.02	49.020	25.980	0.980	24.020
0.03	48.545	26.455	1.455	23.545
0.04	48.080	26.920	1.920	23.080
0.05	47.625	27.375	2.375	22.625
0.06	47.180	27.820	2.820	22.180
0.07	46.745	28.255	3.255	21.745
0.08	46.320	28.680	3.680	21.320
0.09	45.905	29.095	4.095	20.905
0.10	45.500	29.500	4.500	20.500
0.11	45.105	29.895	4.895	20.105
0.12	44.720	30.280	5.280	19.720
0.13	44.345	30.655	5.655	19.345
0.14	43.980	31.020	6.020	18.980
0.15	43.625	31.375	6.375	18.625
0.16	43.280	31.720	6.720	18.280
0.17	42.945	32.055	7.055	17.945
0.18	42.620	32.380	7.380	17.620
0.19	42.305	32.695	7.695	17.305
0.20	42.000	33.000	8.000	17.000
0.21	41.705	33.295	8.295	16.705
0.22	41.420	33.580	8.580	16.420
0.23	41.145	33.855	8.855	16.145
0.24	40.880	34.120	9.120	15.880
0.25	40.625	34.375	9.375	15.625
0.26	40.380	34.620	9.620	15.380
0.27	40.145	34.855	9.855	15.145
0.28	39.920	35.080	10.080	14.920
0.29	39.705	35.295	10.295	14.705
0.30	39.500	35.500	10.500	14.500
0.31	39.305	35.695	10.695	14.305
0.32	39.120	35.880	10.880	14.120
0.33	38.945	36.055	11.055	13.945
0.34	38.780	36.220	11.220	13.780
0.35	38.625	36.375	11.375	13.625
0.36	38.480	36.520	11.520	13.480
0.37	38.345	36.655	11.655	13.345
0.38	38.220	36.780	11.780	13.220
0.39	38.105	36.895	11.895	13.105
0.40	38.000	37.000	12.000	13.000

TABLE 1—(*continued*)

PERCENT CROSSING OVER	PHENOTYPIC CLASSES			
	a *A* SEMISTERILE	b *A* NORMAL	c *a* SEMISTERILE	d *a* NORMAL
0.41	37.905	37.095	12.095	12.905
0.42	37.820	37.180	12.180	12.820
0.43	37.745	37.255	12.255	12.745
0.44	37.680	37.320	12.320	12.680
0.45	37.625	37.375	12.375	12.625
0.46	37.580	37.420	12.420	12.580
0.47	37.545	37.455	12.455	12.545
0.48	37.520	37.480	12.480	12.520
0.49	37.505	37.495	12.495	12.505
0.50	37.500	37.500	12.500	12.500
0.51	37.505	37.495	12.495	12.505
0.52	37.520	37.480	12.480	12.520
0.53	37.545	37.455	12.455	12.545
0.54	37.580	37.420	12.420	12.580
0.55	37.625	37.375	12.375	12.625

and the frequencies must be found by substituting (1-p) for p in the repulsion formulae.

At complete linkage in repulsion the percentage of the normals which are homozygous for the interchange is 0 percent in the *A* and 100 percent in the *a* F_2 phenotype and in coupling is 100 percent in the *A* and 0 percent in the *a* F_2 phenotype.

The percentage phenotypic frequencies expected in F_2 for coupling or for repulsion corresponding to recombination values ranging from 0–55 percent are given in table 1.

It may be noted that at complete linkage the F_2 ratio for the four phenotypes a:b:c:d is 2:1:0:1, while at 50 percent recombination or independence, the ratio is 3:3:1:1.

To determine the percentage of recombination from F_2 data the product method may be used. To facilitate this calculation the $\frac{bc}{ad}$ ratios corresponding to recombination values from 0–55 percent have been calculated and are given in table 2. This table also contains the factors to be divided by $\sqrt{n}$ to obtain the standard error.

The standard error formula for these values may be developed according to the maximum likelihood method given by FISHER (1932) and MATHER (1938 pp. 56–9) as follows:

$$SE = \sqrt{\frac{1}{I}} = \sqrt{\frac{1}{n\,S\,(i)}}, \qquad (1)$$

TABLE 2

Table to facilitate use of the product method in calculating the percentage of recombination from F_2 data involving semisterility and a simply inherited character pair; bc/ad are used for both coupling and repulsion. The last column contains factors to facilitate calculation of the standard error.

PERCENT CROSSING OVER	RATIO OF PRODUCTS $\frac{bc}{ad}$	FACTOR TO BE DIVIDED BY $\sqrt{n}$ TO OBTAIN STANDARD ERROR
0.01	0.010403	0.1402
0.02	0.02162	0.1968
0.03	0.03368	0.2397
0.04	0.04658	0.2756
0.05	0.06034	0.3073
0.06	0.07497	0.3363
0.07	0.09048	0.3632
0.08	0.1069	0.3888
0.09	0.1242	0.4133
0.10	0.1423	0.4373
0.11	0.1614	0.4608
0.12	0.1813	0.4841
0.13	0.2021	0.5074
0.14	0.2237	0.5309
0.15	0.2462	0.5546
0.16	0.2694	0.5789
0.17	0.2935	0.6037
0.18	0.3182	0.6293
0.19	0.3437	0.6558
0.20	0.3697	0.6834
0.21	0.3964	0.7122
0.22	0.4236	0.7425
0.23	0.4512	0.7745
0.24	0.4793	0.8083
0.25	0.5077	0.8444
0.26	0.5363	0.8831
0.27	0.5650	0.9246
0.28	0.5937	0.9696
0.29	0.6223	1.0184
0.30	0.6508	1.0716
0.31	0.6790	1.1302
0.32	0.7067	1.1949
0.33	0.7339	1.2658
0.34	0.7605	1.3476
0.35	0.7862	1.4388
0.36	0.8111	1.5428
0.37	0.8349	1.6625
0.38	0.8575	1.8019
0.39	0.8788	1.9664
0.40	0.8988	2.1637
0.41	0.9172	2.4046
0.42	0.9340	2.7056
0.43	0.9491	3.0925

TABLE 2—(*continued*)

PERCENT CROSSING OVER	RATIO OF PRODUCTS $\frac{bc}{ad}$	FACTOR TO BE DIVIDED BY $\sqrt{n}$ TO OBTAIN STANDARD ERROR
0.44	0.9623	3.6080
0.45	0.9737	4.3299
0.46	0.9831	5.4125
0.47	0.9904	7.2163
0.48	0.9957	10.8255
0.49	0.9989	21.6525
0.50	1.0000	∞
0.51	0.9989	21.6525
0.52	0.9957	10.8255
0.53	0.9904	7.2163
0.54	0.9831	5.4125
0.55	0.9737	4.3299

where I, the total information per F_2 population is n S (i), i is the relative amount of information furnished per each phenotypic class, S the sum, S (i) being the average information per individual in the F_2 population, and n the number of F_2 individuals.

Then $\sqrt{\frac{1}{S\,(i)}}$ is a factor which can be divided by $\sqrt{n}$ to obtain the standard error. This factor can be derived as follows:

$$S\,(i) = S\left(\frac{1}{m} \times \left(\frac{dm}{dp}\right)^2\right) \qquad (2)$$

where m is the expected proportion of the total and dm/dp is the derivative of m with respect to p. The derivation may be tabulated as follows:

F_2 Class	m	$\frac{dm}{dp}$;	$\left(\frac{dm}{dp}\right)^2 \times \frac{1}{m}$	= i in each class
a	$\frac{2-2p+2p^2}{4}$	$\frac{-1+2p}{2}$	$\frac{1-4p+4p^2}{4} \times \frac{4}{2-2p+2p^2}$	$= \frac{1-4p+4p^2}{2-2p+2p^2}$
b	$\frac{1+2p-2p^2}{4}$	$\frac{1-2p}{2}$	$\frac{1-4p+4p^2}{4} \times \frac{4}{1+2p-2p^2}$	$= \frac{1-4p+4p^2}{1+2p-2p^2}$
c	$\frac{2p-2p^2}{4}$	$\frac{1-2p}{2}$	$\frac{1-4p+4p^2}{4} \times \frac{4}{2p-2p^2}$	$= \frac{1-4p+4p^2}{2p-2p^2}$
d	$\frac{1-2p+2p^2}{4}$	$\frac{-1+2p}{2}$	$\frac{1-4p+4p^2}{4} \times \frac{4}{1-2p+2p^2}$	$= \frac{1-4p+4p^2}{1-2p+2p^2}$

Then S (*i*) in formula (2) above is the total of the last column.

As for other F_2 ratios in which the product method has been used, the standard error thus derived for this special case is the same as that derived directly from the product method (HERBERT H. KRAMER unpublished).

The relative information (*i*) for each class can be calculated separately.

Since the relative amounts of information contributed by each phenotypic class may be used as a guide for planning F_2 and F_3 studies they are also included in table 3.

TABLE 3

Relative amounts of information (i) in the four F_2 phenotypic classes together with the average amount of information per F_2 individual S (i) in cases involving semisterility and a simply inherited character pair—same for coupling or repulsion.

PERCENT CROSSING OVER	RELATIVE AMOUNT OF INFORMATION (i) IN EACH PHENOTYPIC CLASS				AVERAGE AMOUNT OF INFORMATION PER F_2 INDIVIDUAL*
	a	b	c	d	S (i)
0.00	0.500	1.000	∞	1.000	∞
0.01	0.485	0.942	48.505	0.980	50.912
0.02	0.470	0.887	23.510	0.960	25.827
0.03	0.455	0.835	15.182	0.938	17.410
0.04	0.440	0.786	11.021	0.917	13.164
0.05	0.425	0.740	8.526	0.895	10.586
0.06	0.410	0.696	6.865	0.873	8.844
0.07	0.396	0.654	5.680	0.850	7.580
0.08	0.381	0.615	4.793	0.827	6.615
0.09	0.366	0.578	4.105	0.804	5.853
0.10	0.352	0.542	3.556	0.780	5.230
0.11	0.337	0.509	3.107	0.757	4.710
0.12	0.323	0.477	2.735	0.732	4.267
0.13	0.309	0.447	2.421	0.708	3.885
0.14	0.295	0.418	2.153	0.683	3.549
0.15	0.281	0.390	1.922	0.658	3.251
0.16	0.267	0.364	1.720	0.632	2.983
0.17	0.254	0.340	1.544	0.607	2.745
0.18	0.240	0.316	1.388	0.581	2.525
0.19	0.227	0.294	1.249	0.555	2.325
0.20	0.214	0.273	1.125	0.529	2.141
0.21	0.202	0.253	1.014	0.503	1.972
0.22	0.189	0.233	0.914	0.477	1.813
0.23	0.177	0.215	0.823	0.451	1.666
0.24	0.165	0.198	0.741	0.426	1.530
0.25	0.154	0.182	0.667	0.400	1.403
0.26	0.143	0.166	0.599	0.374	1.282
0.27	0.132	0.152	0.537	0.349	1.170
0.28	0.121	0.138	0.480	0.324	1.063
0.29	0.111	0.125	0.428	0.300	0.964
0.30	0.101	0.113	0.381	0.276	0.871

TABLE 3—(*continued*)

PERCENT CROSSING OVER	RELATIVE AMOUNT OF INFORMATION (i) IN EACH PHENOTYPIC CLASS				AVERAGE AMOUNT OF INFORMATION PER F_2 INDIVIDUAL*
	a	b	c	d	S (i)
0.31	0.092	0.101	0.338	0.252	0.783
0.32	0.083	0.090	0.298	0.229	0.700
0.33	0.074	0.081	0.261	0.207	0.623
0.34	0.066	0.071	0.228	0.186	0.551
0.35	0.058	0.062	0.198	0.165	0.483
0.36	0.051	0.054	0.170	0.145	0.420
0.37	0.044	0.046	0.145	0.127	0.362
0.38	0.038	0.039	0.122	0.109	0.308
0.39	0.032	0.033	0.102	0.092	0.259
0.40	0.026	0.027	0.083	0.077	0.213
0.41	0.021	0.022	0.067	0.063	0.173
0.42	0.017	0.017	0.052	0.050	0.136
0.43	0.013	0.013	0.040	0.038	0.104
0.44	0.010	0.010	0.029	0.028	0.077
0.45	0.007	0.007	0.020	0.020	0.054
0.46	0.004	0.004	0.013	0.013	0.034
0.47	0.002	0.002	0.007	0.007	0.018
0.48	0.001	0.001	0.003	0.003	0.008
0.49	0.000+	0.000+	0.000+	0.000+	0.000+
0.50	0.000+	0.000+	0.000+	0.000+	0.000+
0.51	0.000+	0.000+	0.000+	0.000+	0.000+
0.52	0.001	0.001	0.003	0.003	0.008
0.53	0.002	0.002	0.007	0.007	0.018
0.54	0.004	0.004	0.013	0.013	0.034
0.55	0.007	0.007	0.020	0.020	0.054

* "Average" is used here in relation to the total information, S (I), only, and does not represent an average of the relative amounts of information (i) in each phenotypic class.

It will be noted that the recessive *a* (classes c and d in table 3) furnishes much more information than does the *A* phenotype (classes a and b in table 3) particularly with close linkage. Hence the classification for sterility of part of the *A* and all of the *a* phenotype would be the most efficient.

INHERITANCE OF PARTIAL STERILITY IN BARLEY

Seed of the partially sterile line of barley, translocation A (SMITH 1941) was furnished by him. The writer is also indebted to DR. M. T. HENDERSON who provided seed grown at University Farm, St. Paul, from the F_1 plants of crosses he had made between the translocation and certain linkage tester stocks.

The genetic make-up of the parents and the linkage group to which each character belongs, based on the summary of genetic studies published by ROBERTSON, WIEBE and IMMER (1941) are as follows:

LINKAGE GROUP	CHARACTER	SYMBOLS	TRANSLOCATION A	COLSESS	BRACHYTIC
I	two vs. six-row	*Vv*	*vv*	*vv*	*VV*
II	black vs. white pericarp and lemma	*Bb*	*bb*	*bb*	*BB*
III	covered vs. naked caryopsis	*Nn*	*nn*	*NN*	*nn*
IV	hooded vs. awned	*Kk*	*kk*	*KK*	*kk*
V	long vs. short haired rachilla	*Ss*	*ss*	*SS*	*SS*
VII	normal vs. brachytic growth	*Br br*	*Br Br*	*Br Br*	*br br*

The Colsess plants had a 2:1 chance of carrying the lethal character xantha seedlings (*xc*) (group VI) but the plant used in the cross proved not to be heterozygous.

The F_2 generation was grown in the field at University Farm, St. Paul, in 1944. Cold weather delayed planting until extremely late and was followed by a relatively dry period with higher temperatures which did not favor the production of strong vigorous plants in this apparently unadapted material. For pollen examination 2–3 florets from each individual plant were removed just previous to pollen shedding and placed in a vial of 70 percent ethyl alcohol. Classification of these fieldgrown plants for pollen sterility was difficult, very few of them showing completely filled normal pollen grains. Partially sterile plants were recognized by the presence of an estimated 30 percent of smaller shrivelled empty pollen grains. Classification of plants grown in the greenhouse was more satisfactory.

Since the F_1 had not been classified previously for sterility, F_2 progenies were grown from each F_1 plant. Only part of them were expected to be segregating for sterility. Since in corn the ratio of semisteriles to normals is approximately 1:1 (BRINK and BURNHAM 1929, BURNHAM 1934), a similar ratio was assumed for barley. When as many as ten plants of a progeny had been examined in an F_2 culture without locating any partially sterile ones, the culture was discarded.

The following tabulation shows the number of partially sterile and normal plants obtained in the F_2 and the P values for the χ^2 test of goodness of fit to a 1:1 ratio.

CROSS	PARTIALLY STERILES	NORMALS	χ^2	P
37 (field and greenhouse)	36	50	2.280	0.2–0.1
38 (field only)	88	134	9.532	<0.01
39 (field only)	78	160	28.252	<0.01

The 21 plants from cross 37 which had been grown and classified in the field were checked in F_3 in the greenhouse. Of the 11 classed as normal in the field,

6 were actually partially sterile; while of the 10 classed as partially sterile in the field 2 were normal, the corrected figures being 7 normals and 14 partially steriles. The excess of normals in the field grown plants in cross 37 is accounted for by the larger error in classifying the normals; yet there was a similar excess of normals in the greenhousegrown plants which appeared to be classified with ease. In the F_2 population corrected on the basis of F_3 progeny tests, there was an excess of partially steriles. Further experiments are needed to determine the exact ratio of normals to partially sterile plants.

A summary of the F_2 linkage data obtained in the different cultures of crosses 37, 38 and 39 together with the P values corresponding to the χ^2 tests of independence (FISHER'S short method) are given in table 4. All the data are in repulsion.

TABLE 4

Summary of linkage data between partial sterility vs. normal and various character pairs designated A vs. a in barley. P values for the χ^2 tests for independence are included.

CROSS	CHARACTER *Aa*	PARTIALLY* STERILE *A*	NORMAL *A*	PARTIALLY STERILE *a*	NORMAL *a*	TOTAL	P VALUE
37	*Vv*	34	31	2	19	86	<0.01
	Ss	9	5	5	2	21	0.70
	Bb	11	6	2	1	20	0.95
38	*Kk*	66	95	22	39	222	0.50
	Ss	62	95	26	35	218	0.70
	Nn	63	68	26	43	200	0.20–0.10
39	*Kk*	57	117	21	43	238	0.99
	Ss	61	116	17	41	235	0.50
	Nn	27	37	13	15	92	0.70

* Partial sterility vs. normal is the *Bb* character pair in the previous tables.

Cross 37 was segregating *br* also, but the character could not be classified satisfactorily.

No association is indicated between partial sterility and *Ss*, *Bb*, *Kk* and *Nn*, based on the fieldgrown F_2 plants. In spite of the difficulties in sterility classification, any close linkage should have been detected. Association is indicated only between partial sterility and the two-row vs. six-row character pair (*Vv*). The data for this character pair were derived from the fieldgrown F_2 plants checked for sterility classification in F_3, and additional F_2 type data from F_3 populations, grown from partially sterile *Vv* F_2 plants. Even in the small F_2 fieldgrown populations, there was evidence suggesting linkage, the numbers in the four phenotypes being: 8:4:2:7. (P=0.05.) The numbers corrected on the basis of F_3 data were 14:3:0:4.

Division of the χ^2 test for goodness of fit into its components for the *Vv* data of table 4 based on a 3:3:1:1 ratio gives the following P values:

Vv segregation	P=0.90
Sterility	P=0.10
Linkage	P<0.01

The P values for the *Vv* and sterility segregations indicate satisfactory fits while the P value of less than 0.01 for the other component again indicates linkage.

The degree of linkage indicated by the F_2 data was calculated by using the product method, assuming that sterility segregated in a 1:1 ratio, the ratio bc/ad being 0.096 which according to table 2 corresponds to a recombination value of 7 ± 3.9 percent, the SE also being determined from the same table.

Where several normally independently inherited qualitative character pairs segregate along with partial sterility, a linkage between any two of the qualitative ones should indicate the two linkage groups involved in the translocation. These data are not affected by errors in classification for sterility.

Such tests between *Vv*, *Ss* and *Bb* in cross 37 based on small numbers; and between *Kk*, *Ss* and *Nn* in crosses 38 and 39 summarized in table 5 show independence in all cases.

TABLE 5

Summary of observed segregation for qualitative character pairs in the F_2 progeny of partially sterile F_2 plants, together with the P values obtained from the χ^2 tests for independence.

CHARACTER PAIRS	F_2 PHENOTYPES				TOTAL n	P
	a	b	c	d		
Cross 37						
Vv—*Bb*	20	5	4	1	30	0.99
Vv—*Ss*	21	5	3	2	31	0.30
Bb—*Ss*	17	7	3	3	30	0.50–0.30
Crosses 38, 39						
Kk—*Ss*	123	50	43	18	234	0.95
Kk—*Ss*	139	49	56	15	259	0.50–0.30
Kk—*Nn*	106	51	37	21	215	0.70
Kk—*Nn*	46	24	18	6	94	0.50–0.30
Ss—*Nn*	99	52	38	23	212	0.70
Ss—*Nn*	46	26	20	4	96	0.10–0.05

The second linkage group involved in the translocation remains, therefore, to be identified.

Meiosis of partially sterile plants was studied by the acetocarmine smear method. A ring of four chromosomes plus five pairs was observed at diakinesis and metaphase I. Diakinesis figures showed that the ring does not include the chromosome which is attached to the nucleolus and which bears the large satellite.

SUMMARY

Formulae were derived for the expected genotypic and phenotypic frequencies in F_2 populations involving linkage between semisterility and a qualitative character showing 3:1 segregation.

Table 1 contains the F_2 percentage frequencies for the four phenotypic classes with recombination values from 0–55 percent, the frequencies being the same for coupling or repulsion.

To facilitate the calculation of linkage intensities by the product method the ratios of products bc/ad and the factors to be divided by $\sqrt{n}$ to obtain the standard errors for recombination values from 0–55 percent for coupling or for repulsion were calculated (table 2).

Table 3 contains the relative amounts of information for each of the four F_2 phenotypic classes (i) and the average amounts of information per F_2 individual S (i) for recombination values from 0–55 percent.

Partially sterile plants from SMITH's translocation A stock were found to have a ring of four chromosomes plus five pairs in agreement with his findings. The chromosome which is attached to the nucleolus and which bears the large satellite is not involved in the ring.

The ratio of normal to partially sterile plants in the progeny of a partially sterile plant deviated from the expected 1:1 ratio, but further data are needed to determine the actual breeding behavior.

Partial sterility showed no linkage with the following characters: black vs. white pericarp and lemma (*Bb*), hooded vs. awned (*Kk*), long vs. short haired rachilla (*Ss*) and covered vs. naked caryopsis (*Nn*).

Partial sterility was found to be linked with the character pair two-row vs. six-row (*Vv*) in linkage group 1 the recombination value for F_2 data in repulsion by the product method being 7 ± 3.9 percent. The second linkage group involved remains to be identified.

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A SEARCH FOR SEX GENES IN THE SECOND CHROMOSOME OF DROSOPHILA MELANOGASTER USING THE TRIPLOID METHOD

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THE male determining influence of the autosomes on sex differentiation in *Drosophila melanogaster* was proven by BRIDGES in 1921 with the discovery of triploid intersexes. He found that individuals with two X chromosomes, as in diploid females, and three of each autosome (3A) develop intersexually. BRIDGES concluded that sex is determined by an interplay of female determining genes located principally in the X chromosome and male determining genes located principally in the autosomes.

The question of a single sex gene versus multiple sex genes in the X chromosome of *Drosophila melanogaster* was debated by investigators for a number of years. PATTERSON, with his gynandromorph experiments in 1931, restricted a possible female determining sex factor to the garnet-forked region of the X chromosome. In later experiments, using hyperdiploid males; i.e., those carrying in excess a short fragment of the X chromosome, PATTERSON, STONE and BEDICHEK (1937) eliminated all regions of the X chromosome as a possible site of a primary female sex gene except the wavy-garnet region. In 1938, PATTERSON narrowed this region to the garnet-pleated section, between salivary gland bands 13 A2 and 13 A6. Males hyperploid for this region failed to live. MULLER (1930) and DOBZHANSKY and SCHULTZ (1934) made observations on certain diploid aneuploids with regard to presence of a possible female sex gene(s) in the X chromosome.

In 1934 DOBZHANSKY and SCHULTZ presented results of their studies of sex balance in certain sections of the X chromosome. They crossed hyperdiploid males and also X,4 translocation males to triploids homozygous for recessive X chromosome marker genes. This method, originally suggested by MULLER and STONE (1930), allowed the authors to observe the effects of adding extra fragments of the X chromosome to the intersex chromosome complement (2X3A). DOBZHANSKY and SCHULTZ showed that the addition of certain long fragments of the X chromosome to the 2X3A intersex complement resulted in hypotriploid females of reduced fertility. The shortest section which nevertheless produced a weakly fertile hypotriploid female when added to the 2X3A chromosome set was duplication L.V.M., a section covering the *y-pn* plus *fu-bb* regions. Very short sections from the extreme left as well as very short sections including both right and left ends of the X chromosome produced slight shifts in the mean sex type of the duplication intersexes in the female direction.

PIPKIN (1940) studied different duplication intersexes possessing 2X3A and a short section of each region of the X chromosome. Small shifts of sex type

in the female direction were observed in three cases; no shifts, in two cases. Longer sections of the X chromosome added to the 2X3A chromosome complement produced decided shifts in the female direction. Either the left or right hand fragment of the w-13 translocation, broken approximately at salivary gland band 9B1, when added to 2X3A, produced a hypotriploid female of extremely low fertility. A somewhat shorter fragment of the left hand part of the X chromosome sufficed to transform a duplication intersex (hyperintersex) into a hypotriploid female with ability, however weak, of producing a functional egg.

PATTERSON, BROWN, and STONE (1940) performed diploid aneuploid studies in both chromosomes 2 and 3 similar to those involving chromosome 2 in the present study with triploids. Hyperdiploid males and females were obtained for short sections covering the entire chromosomes 2 and 3. In no case was any shift toward maleness observed in a hyperdiploid female, although fertility and viability were reduced in varying degrees in aneuploids of both sexes.

No extensive work on triploid aneuploidy involving autosomes has hitherto been reported. MORGAN, BRIDGES, and SCHULTZ (1930) mention a hypotriploid female with a small deficiency in the *pr* region.

Two autosomal mutations shifting sex have been described in *Drosophila melanogaster*. L. V. Morgan (in Morgan, Redfield, and Morgan, 1943) found a recessive gene in chromosome 2 which causes diploid females to become intersexual. Sturtevant (1945) discovered a recessive gene in chromosome 3 which transforms diploid females into sterile males.

Autosomal male determining mutations have also been reported in *Drosophila virilis*. LEBEDEFF (1939) described a recessive autosomal gene, *ix*, which causes homozygous diploid females to become intersexual. NEWBY (1942) studied a dominant autosomal mutant in the Blanco stock of *D. virilis* which likewise converts diploid females into intersexes.

Drosophila neorepleta carries an autosomal gene which, when present in single dose in a hybrid female of a cross with *D. repleta*, makes her eggs male in potentiality. Two *repleta* X chromosomes in such eggs result in development of male-like intersexes (STURTEVANT, 1946).

The purpose of the present study is to use the triploid method in a search for possible male sex genes or sexually potent sections of chromosome 2 of *D. melanogaster*.

MATERIALS AND METHODS

The translocation stocks used in the present investigation involved mutual interchange between chromosome 2 and the short chromosome 4. Nine 2, 4 translocation stocks were employed: T8, T45, T53, T4, T29, T30, T34, and T6. The genetic and cytological points of breakage of these translocations are shown in table 1. The translocations were produced by X-radiation and their breakage points analyzed genetically by PATTERSON, STONE, BEDICHEK, and SUCHE (1934). The cytological analysis of their breakage points was made by PAINTER (1934) and GRIFFEN (unpublished).

TABLE 1

Genetic and cytological points of breakage of 2,4 translocation stocks.

STOCK NUMBER	GENETIC BREAKAGE POINT	CYTOLOGICAL BREAKAGE POINT (BAND NUMBERS OF BRIDGES' 1935 SALIVARY MAP GIVEN)	
T8	dumpy-black	26F-4	27A-1
T45	black-purple	36D-3	
T53	black-purple	36E-1	36E-3
T4	purple-curved	chromocenter	
T29	purple-curved	47A-4	47A-5
T40	purple-curved	49F-3	50A-1
T30	purple-curved	53B-2	53C-1
T34	curved-plexus	56F-6	56F-7
T6	plexus-speck	57F-2	57F-3

Two triploid stocks were used: a vigorous y^2; *b sp* (yellow-2; black speck) triploid strain served to test all regions of the right arm of chromosome 2. A triploid strain homozygous for y^2; *al sp* (yellow-2; aristaless speck), but less vigorous, was required to test all regions of the left arm of chromosome 2.

In order to study intersexes or other triploid aneuploids bearing in excess or deficient for a right hand end region, males carrying the translocation and

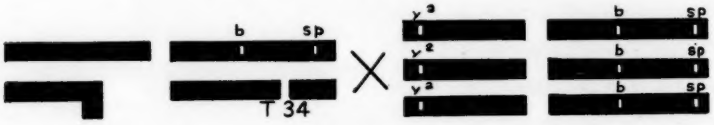

FIGURE 1a

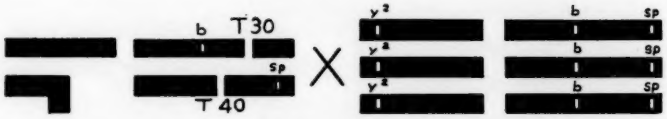

FIGURE 1b

also a normal chromosome 2 marked with *b* and *sp* were crossed with triploids homozygous for y^2; *b sp*. For left arm end regions, males heterozygous for the translocation and a normal 2 marked with *al sp* were crossed with y^2; *al sp* triploids. These crosses are shown in diagrammatic form in fig. 1a.

To study triploid aneuploidy of interior regions, males heterozygous for two translocations, the points of breakage of which were of varying distances apart depending upon the region studied were crossed with y^2; *al sp* triploids, if a left arm region was being studied; y^2; *b sp* triploids, if a right arm region

was being studied. A diagram of this type of cross appears in fig. 1b. In all but two of the crosses designed for studying triploid aneuploidy of interior regions, there was one recessive marker on each translocation in the heterozygous translocation male parents rather than two recessive markers on the one translocation and only wild type alleles on the other translocation. The former cross is more efficient so far as viability of aneuploid progeny as well as identification of all aneuploids is concerned.

The X chromosome recessive marker gene, y^2, was introduced into the basic triploid strains in order to identify positively intersexes receiving two X chromosomes from the female triploid parent. Actually such intersexes are in the minority as BEADLE (1935) has pointed out on account of non-random disjunction of X chromosomes and autosomes during meiosis in the triploid female. As a result, y^2 hyper-or hypointersexes were not recovered in all experimental crosses in which corresponding hyper- or hypointersexes not homozygous for y^2 nevertheless appeared. The most important function of y^2 was to increase the vigor of the triploid strains. Although no tests with isogenic stocks have been made, it is the experience of the author that triploid stocks homozygous for y^2 are far more vigorous than those without it.

According to fig. 1a, a cross of males heterozygous for translocation T34, carrying wild type alleles and a normal chromosome 2 carrying the recessive marker genes *b sp* with triploid females homozygous for y^2; *b sp* yields euploid 3A progeny of the following types: wild type triploid females; *b sp* triploid females (3X3A); wild type intersexes, *b sp* intersexes, y^2 intersexes, y^2; *b sp* intersexes (2X3A). As in previous literature on polyploidy, 2X indicates two X chromosomes; 3A, three of each autosome. The aneuploid 3A progeny include *b* hypertriploid females with three X chromosomes, three chromosomes 3, three chromosomes 2, and the short right hand fragment of translocation T34; i.e., T34R. The normal allele of *sp*, present in T34R is dominant over the recessive marker gene *sp* present in each of the three normal chromosomes 2 in this hypertriploid female. In addition the *sp* hypotriploid female appears in the progeny of this cross under discussion. This hypotriploid contains three X chromosomes, three chromosomes 3, two chromosomes 2, each bearing the recessive marker genes *b sp*, and the long left hand fragment of translocation T34; i.e., T34L. The *b* hyperintersex appearing in the progeny of this cross contains an X chromosome bearing the normal allele of y^2, a y^2 X chromosome, three chromosomes 3, three chromosomes 2, each bearing *b sp*, and T34R, the right hand fragment of translocation T34. The y^2; *b* hyperintersex possesses two X chromosomes, each bearing y^2, three chromosomes 3, three chromosomes 2, each bearing *b sp*, and T34R, the right hand fragment of translocation T34. No hypointersexes survived among the progeny of this cross.

As an illustration of the second type of experimental cross, fig. 1b shows males heterozygous for translocation T40 and translocation T30 crossed with y^2; *b sp* triploids. Translocation T40 carried the recessive marker gene *sp*; translocation T30, the recessive marker gene *b*. The 3A aneuploid progeny include *b sp* hypertriploid females carrying three X chromosomes, three chromosomes 3, two chromosomes 2 each bearing *b sp*, the left hand fragment of

TABLE 2

3A progeny of males heterozygous for a single translocation crossed with y^2; al sp (or y^2; b sp) triploids: study of end regions of chromosome 2.

(a) 3A euploid progeny

P_1 ♂	+/y^2/y^2; T/*al* *sp*/*al* *sp*	+/y^2/y^2; *al sp*/*al* *sp*/*al* *sp*	+/y^2; T/*al* *sp*/*al* *sp*					+/y^2; *al sp*/*al* *sp*/*al* *sp*					y^2/y^2; T/*al* *sp*/*al* *sp*					y^2/y^2; *al sp*/*al* *sp*/*al* *sp*				
	WILD TYPE TRIPLOID	*al sp* TRIPLOID	WILD TYPE INTERSEX					*al sp* INTERSEX					y^2 INTERSEX					y^2; *al sp* INTERSEX				
			I	II	III	IV	V	I	II	III	IV	V	I	II	III	IV	V	I	II	III	IV	V
T8/*al sp*	40	32	3	10	29	52	6	1	12	25	30	1	—	—	4	7	4	—	2	6	4	2

(a) *continued*

P_1 ♂	+/y^2/y^2; T/*b* *sp*/*b* *sp*	+/y^2/y^2; *b sp*/*b* *sp*/*b* *sp*	+/y^2; T/*b* *sp*/*b* *sp*					+/y^2; *b sp*/*b* *sp*/*b* *sp*					y^2/y^2; T/*b* *sp*/*b* *sp*					y^2/y^2; *b sp*/*b* *sp*/*b* *sp*				
	WILD TYPE TRIPLOID	*b sp* TRIPLOID	WILD TYPE INTERSEX					*b sp* INTERSEX					y^2 INTERSEX					y^2 *b sp* INTERREX				
			I	II	III	IV	V	I	II	III	IV	V	I	II	III	IV	V	I	II	III	IV	V
T29/*b sp*	23	28	7	7	—	16	4	3	7	9	17	2	—	2	2	2	—	1	4	1	4	1
T40/*b sp*	44	35	3	16	30	19	—	0	7	19	14	1	2	5	7	6	1	1	1	8	2	—
T30/*b sp*	89	76	26	29	54	67	10	18	21	27	35	7	5	8	19	10	1	2	3	9	4	1
T34/*b sp*	66	65	13	21	26	19	1	11	3	30	19	5	7	3	7	1	1	1	3	9	2	—
T6/*b sp*	68	79	25	50	49	20	1	15	24	40	15	—	2	0	25	5	—	1	3	12	4	—

(b) 3A aneuploid progeny.

P_1 ♂	+/y^2/y^2; *L*/*al* *sp*/*al* *sp*/*al* *sp*	+/y^2/y^2; R/*al* *sp*/*al* *sp*	+/y^2; *L*/*al* *sp*/*al* *sp*/*al* *sp*				
	sp HYPERTRIPLOID	*al sp* HYPOTRIPLOID	*sp* HYPERINTERSEX				
			I	II	III	IV	V
T8/*al sp*	6	6	1	1	5	—	—

(b) *continued*.

P_1 ♂	+/y^2/y^2; R/*b* *sp*/*b* *sp*/*b* *sp*	+/y^2/y^2 L/*b* *sp*/*b* *sp*	+/y^2; R/*b* *sp*/*b* *sp*/*b* *sp*					y^2/y^2; R/*b* *sp*/*b* *sp*/*b* *sp*					+/y^2; L/*b* *sp*/*b* *sp*				
	b HYPERTRIPLOID	*sp* HYPOTRIPLOID	*b* HYPERINTERSEX					y^2; *b* HYPERINTERSEX					*sp* HYPOINTERSEX				
			I	II	III	IV	V	I	II	III	IV	V	I	II	III	IV	V
T29/*b sp*	2(?)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
T40/*b sp*	3(?)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
T30/*b sp*	15	2	1	3	6	4	—	—	1	1	1	—	—	—	—	—	—
T34/*b sp*	14	27	1	—	3	—	—	1	1	1	—	—	—	—	—	—	—
T6/*b sp*	10	52	10	14	10	2	—	2	—	5	—	—	—	—	—	1	—

translocation T30 carrying the recessive marker gene *b* and the right hand fragment of translocation T40, carrying the recessive marker gene *sp*. The wild type hypotriploid females occurring in the progeny of this cross possess three X chromosomes, three chromosomes 3, two chromosomes 2, the left hand fragment of translocation T40, bearing the normal allele of *b*, and the right hand fragment of translocation T30, bearing the normal allele of *sp*. Hyperintersexes appearing *b sp* (and y^2; *b sp*) have two X chromosomes, three chromosomes 3, two *b sp* chromosomes 2, the left hand fragment of translocation T30 carrying *b* and the right hand fragment of translocation T40 carrying *sp*. The wild type hypointersexes possess two X chromosomes, three chromosomes 3, two chromosomes 2 carrying *b sp*, the left hand fragment of translocation T40, bearing the normal allele of *b*, and the right hand fragment of translocation T30, carrying the normal allele of *sp*.

Experimental crosses were made in mass cultures in half pint milk bottles, seven triploid females and about 20 males to the bottle. Cultures were kept in an incubator at about 22°C, but temperatures occasionally varied as much as two degrees above and two degrees below 22°C. For this reason, counts were made of each bottle separately so that homogeneity tests might be made to determine if environmental differences were sufficient to alter the proportions of the five sex type groups of intersexes coming from different bottles.

EXPERIMENTAL RESULTS

In table 2 appear the triploid and intersexual progeny of males heterozygous for a 2, 4, translocation and a normal *b sp* (or *al sp*) chromosome with y^2; *b sp* (or y^2; *al sp*) triploids, respectively. This method, previously described, is designed for studying end regions of chromosome 2. Table 2a gives euploid 3A progeny; table 2b, the 3A aneuploid progeny. A record was kept of all diploid progeny from each experimental bottle, but these are not included in the present study since PATTERSON, BROWN, and STONE (1940) have made an exhaustive investigation of diploid aneuploidy of 2 using the same translocation stocks as the present author.

The first column of table 2a gives the chromosome 2 composition of the diploid male parent. The successive columns are headed by the genotype of the 3A progeny they contain, below which appears the phenotype, followed by the number obtained of the respective 3A progeny type. Thus there were 32 *al sp* triploid females of genotype +/y^2/y^2; *al sp*/*al sp*/ *al sp* obtained in the progeny of the cross of T8/ *al sp* males with y^2; *al sp* triploid females. The intersexes are grouped in classes I to V, following DOBZHANSKY and SCHULTZ'S descriptions (1934). No type VI intersexes occurred. Table 2b gives hypertriploids, hypotriploids, hyperintersexes, and hypointersexes, where these appear among the progeny of the crosses described. The letter R indicates the right hand fragment of the respective translocations listed in the first column; L, the corresponding left hand fragment.

In two cases; i.e., from crosses of T29/ *b sp* males with y^2; *b sp* triploids and T40/*b sp* males with y^2: *b sp* triploids, the few *b* 3A aneuploids are presumed

TABLE 3

3A progeny of males heterozygous for two different translocations crossed with y^2; al sp (or y^2; b sp) triploids: study of interior regions of chromosome 2.

(a) 3A euploid progeny.

P1 ♂	+/y^2/y^2; T, *sp*/*al* *sp*/*al* *sp*	+/y^2/y^2; T, *al*/*al* *sp*/*al* *sp*	+/y^2; T, *sp*/*al* *sp*/*al* *sp*					+/y^2; T, *al*/*al* *sp*/*al* *sp*					y^2/y^2; T, *sp*/*al* *sp*/*al* *sp*					y^2/y^2; T, *al*/*al* *sp*/*al* *sp*				
	sp TRIPLOID	*al* TRIPLOID	*sp* INTERSEX					*al* INTERSEX					y^2; *sp* INTERSEX					y^2; *al* INTERSEX				
			I	II	III	IV	V	I	II	III	IV	V	I	II	III	IV	V	I	II	III	IV	V
T8, *sp*/T45, *al*	32	32	3	6	11	22	6	4	10	14	14	3	—	—	4	3	3	—	1	4	3	2
T53, *sp*/T45, *al*	12	12	—	4	7	13	—	1	7	11	7	2	—	—	1	3	1	—	—	2	3	—
T4, *sp*/T53, *al*	48	40	3	8	37	22	4	8	7	26	36	5	—	2	7	6	2	—	—	7	7	1

(a) *continued*

P1 ♂	+/y^2/y^2; T, *sp*/*b* *sp*/*b* *sp*	+/y^2/y^2; T, *b*/*b* *sp*/*b* *sp*	+/y^2; T, *sp*/*b* *sp*/*b* *sp*					+/y^2; T, *b*/*b* *sp*/*b* *sp*					y^2/y^2; T, *sp*/*b* *sp*/*b* *sp*					y^2/y^2; T, *b*/*b* *sp*/*b* *sp*				
	sp TRIPLOID	*b* TRIPLOID	*sp* INTERSEX					*b* INTERSEX					y^2; *sp* INTERSEX					y^2; *b* INTERSEX				
			I	II	III	IV	V	I	II	III	IV	V	I	II	III	IV	V	I	II	III	IV	V
T29, *sp*/T30, *b*	90	84	9	8	23	34	14	14	27	31	59	22	1	4	10	13	1	2	5	20	13	3
T29, *sp*/T34, *b*	32	40	1	6	12	9	—	9	18	13	3	—	3	3	5	2	1	3	3	5	—	—
T40, *sp*/T30, *b*	61	78	29	39	37	20	3	34	40	32	25	1	6	7	15	3	1	4	9	11	8	1
T40, *sp*/T34, *b*	28	15	11	8	13	7	2	9	3	7	5	—	1	1	4	1	—	1	1	3	—	—
T30, *sp*/T34, *b*	54	48	9	15	27	20	3	11	13	14	12	—	—	5	6	4	1	2	1	4	1	—

(b) 3A aneuploid progeny.

P1 ♂	+/y^2/y^2; T, *sp* R+ T, *al* L/*al* *sp*/*al* *sp*	+/y^2/y^2; T L+ T R/*al* *sp*/*al* *sp*	+/y^2; T, *sp* R+T, *al* L/*al* *sp*/*al* *sp*					+/y^2; T L +T R/*al* *sp*/*al* *sp*/*al* *sp*				
	al sp HYPERTRIPLOID	WILD TYPE HYPOTRIPLOID	*al sp* HYPERINTERSEX					WILD TYPE HYPOINTERSEX				
			I	II	III	IV	V	I	II	III	IV	V
T8, *sp*/T45, *al*	17	3	1	—	—	—	1	—	1	—	1	—
T53, *sp*/T45, *al*	1 (wild type)	7 (*al sp*)	—	2	3	2	—	5	2	3	17	—
T4, *sp*/T53, *al*	5 (wild type)	—	2 (wild type)	—	—	—	—	—	—	—	—	—

TABLE 3—(*continued*)

(b) *continued.*

P_1 ♂	+/y^2/y^2; T, *sp* R+T, *b* L/*b sp*/*b sp*	+/y^2/y^2; T L+ TR/*b sp*/*b sp*	+/y^2; T, *sp* R+T, *b* L/*b sp*/*b sp*					+/y^2; T L+T R/*b sp*/*b sp*					y^2/y^2; T, *sp* R+T, *b* L/*b sp*/*b sp*					y^2/y^2; T L+T R/*b sp*/*b sp*
	b sp HYPERTRIPLOID	WILD TYPE HYPOTRIPLOID	*b* ♀ HYPERINTERSEX					WILD TYPE HYPOINTERSEX					y^2; *b sp* HYPERINTERSEX					y^2 HYPOINTERSEX
			I	II	III	IV	V	I	II	III	IV	V	I	II	III	IV	V	IV
T29, *sp*/T30, *b*	17	21	1	5	7	9	1	1	—	—	—	—	—	—	—	—	1	—
T29, *sp*/T34, *b*	30	2	—	1	—	1	—	—	—	1	1	—	—	—	—	—	—	—
T40, *sp*/T30, *b*	20	48	6	12	4	5	—	—	2	—	—	—	1	—	—	—	—	—
T40, *sp*/T/34, *b*	9	1	—	—	1	—	—	—	—	1	—	—	—	—	—	—	—	—
T30, *sp*/T34, *b*	47	6	1	5	4	10	1	—	—	—	1	—	—	—	2	3	—	1

TABLE 4

3A progeny of males heterozygous for two different translocations crossed with y^2; b sp triploids: study of interior regions of chromosome 2.

(a) 3A euploid progeny.

P_1 ♂	+/y^2/y^2; T, *b sp* *b sp*/*b sp*	+/y^2/y^2; T/*b* *sp*/*b sp*	+/y^2; T, *b sp*/*b* *sp*/*b sp*					+/y^2; T/*b* *sp*/*b sp*					y^2/y^2; T, *b sp*/*b* *sp*/*b sp*					y^2/y^2; T/*b* *sp*/*b sp*				
	b,sp TRIPLOID	WILD TYPE TRIPLOID	*b sp* INTERSEX					WILD TYPE INTERSEX					y^2; *b sp* INTERSEX					y^2 INTERSEX				
			I	II	III	IV	V	I	II	III	IV	V	I	II	III	IV	V	I	II	III	IV	V
T4, b *sp*/T29	113	105	59	54	88	42	5	24	26	50	19	1	9	14	33	15	1	4	7	20	6	—
T29/T40, *b sp*	28	36	6	19	28	15	—	7	10	24	24	3	—	2	7	4	—	—	1	4	—	—

(b) 3A aneuploid progeny.

P_1 ♂	+/y^2/y^2; R+L/*b* *sp*/*b sp*	+/y^2/y^2; L+R/*b* *sp*/*b sp*	+/y^2; R+L/*b* *sp*/*b sp*					y^2/y^2; R+L/*b* *sp*/*b sp*					+/y^2; L+R/*b* *sp*/*b sp*					y^2/y^2, L+R/*b* *sp*/*b sp*				
	HYPERTRIPLOID	HYPOTRIPLOID	HYPERINTERSEX					HYPERINTERSEX					HYPOINTERSEX					HYPOINTERSEX				
			I	II	III	IV	V	I	II	III	IV	V	I	II	III	IV	V	I	II	III	IV	V
T4, *b sp*/T29	67 (*sp*)	30 (*b*)	—	—	—	—	—	—	—	—	—	—	12	12 (*b*)	13	7	—	—	2	6 (3^2; *b*)	—	1
T29/T40, *b sp*	40 (*b*)	10 (*sp*)	8	11	17 (*b*)	20	2	—	3	9 (3^2; *b*)	1	3	—	—	1 (*sp*)	—	—	—	—	—	—	—

to be hypertriploids rather than hypotriploids because the former are in most cases far more viable than any other 3A aneuploid type.

Tables 3 and 4 give progeny of males heterozygous for two different translocations with y^2; *al sp* triploids or y^2; *b sp* triploids, depending upon whether or not the breakage points of the translocations are located in the left or right arm of 2. This type of cross, previously described, is designed for studying aneuploids carrying in excess or deficiency an interior region of 2. Table 3a presents 3A euploid progeny; table 3b, 3A aneuploid progeny, respectively. In tables 4a and 4b, euploid and aneuploid progeny are included, respectively.

In certain cases such as aneuploid progeny from a cross of T53, *sp*/T45, *al*

TABLE 5

Summary of presence (+) or absence (−) of 3A aneuploids for various regions of chromosome 2.

ANEUPLOID REGION	CYTOLOGICAL LENGTH IN MILLIMETERS	HYPER-TRIPLOID	HYPO-TRIPLOID	HYPER-INTERSEX	HYPO-INTERSEX
8L	107	+	+	+	−
8–45	200	+	+	+	+
45–53	30	+	+	+	+
53–4	92	+	−	+	−
4–29	132	+	+	−	+
29–40	57	+	+	+	+
40–30	100	+	+	+	+
30–34	75	+	+	+	+
34R	98	+	+	+	−
6R	69	+	+	+	+
29–30	157	+	+	+	+
29–34	232	+	+	+	+
40–34	175	+	+	+	+
30R	173	+	+	+	−

males with y^2; *al sp* triploids, the aneuploid offspring are not of the phenotype indicated at the head of the column. In these cases the correct phenotype is indicated in parenthesis in the body of the table.

In table 5 appears a summary of the presence or absence of 3A aneuploids obtained in tables 2, 3, and 4. Of ten short regions covering the entire chromosome 2, hypertriploid females survived for each region; hypotriploid females, for nine regions; hyperintersexes, for nine regions; and hypointersexes for seven regions. Of four longer regions, there were hypertriploid females, hypotriploid females, and hyperintersexes for each section and hypointersexes for three of the four longer sections. With one exception, the region between translocations T4 and T29, the hypointersexes survived in very few numbers. For this section there were many hypointersexes and no hyperintersexes. This discrepancy is probably not owing to lack of viability on account of fourth chromosome aneuploidy but rather to second chromosome aneuploidy since the hypertriploid females for this region survived twice as frequently as the hypotriploids.

The ratio of hypertriploid females to hypotriploid females obtained from a single cross listed in tables 2, 3, and 4 varied considerably with the region involved. The viability of these aneuploids is probably influenced not only by chromosome 2 but also by chromosome 4 aneuploidy.

In table 6 appear descriptions of the various hypertriploid females obtained, with especial reference to their body size, wings, eyes, and fertility. The first

TABLE 6

Descriptions of hypertriploid females.

REGION IN EXCESS OF THREE CHROMOSOMES 2	CYTOLOGICAL LENGTH IN MILLIMETERS	TABLE NUMBER	BODY SIZE	WINGS	EYES	FERTILITY
8L	107	2b	Shorter and squatter than 3X3A sibs.	Similar to 3X3A sibs.	Similar to 3X3A sibs.	3 F/3
8–45	200	3b	Similar to 3X3A sibs.	Similar to 3X3A sibs.	Similar to 3X3A sibs.	2 F/2
45–53	30	3b	Similar to 3X3A sibs.	Similar to 3X3A sibs.	Similar to 3X3A sibs.	Not tested
53–4	92	3b	About size 2X2A sibs.	Wings held slightly apart.	Similar to 3X3A sibs.	1 F/3
4–29	132	4b	About size 2X2A sib; smaller than hypotriploid sibs.	Sometimes wings clipped slightly on medial edge.	Facets slightly disarranged; eye sometimes narrow; one specimen lacked ocelli.	2 F/31
29–40	57	4b	Slightly larger than 3X3A sibs.	Similar to 3X3A sibs.	Similar to 3X3A sibs.	21 F/23
40–30	100	3b	Similar to 3X3A sibs.	Similar to 3X3A sibs.	Similar to 3X3A sibs.	14 F/16
30–34	75	3b	Similar to 3X3A sibs.	Often wings outstretched; crumpled; reduced in size; one or both cross veins missing; extra short veins; texture fine in abnormal wings.	Similar to 3X3A sibs.	19 F/37
34R	98	2b	About size 2X2A sibs.	Similar to 2X2A sibs.	Facets slightly disarranged.	2 F/7
6R	69	2b	Slightly larger than 3X3A sibs.	Similar to 3X3A sibs.	Similar to 3X3A sibs.	6 F/7
30R	173	2b	About size 2X3A sibs.	Similar to 3X3A sibs.	Facets slightly disarranged.	3 F/11
29–30	157	3b	Similar to 3X3A sibs.	Similar to 3X3A sibs.	Similar to 3X3A sibs.	10 F/12
29–34	232	3b	Similar to 3X3A sibs.	Usually similar to 3X3A sibs; one had extra veins.	Similar to 3X3A sibs.	0 F/20
40–34	175	3b	Usually size 3X3A sibs; one larger and one smaller.	Wings outstretched; one lacked left cross vein.	Similar to 3X3A sibs.	1 F/4

column of table 6 indicates the region carried in excess of three chromosomes 2. For end regions the letters L or R mean left or right hand fragments, respectively. For interior regions the numbers of the translocation are given, the interior regions being between their points of breakage. The second column gives the region length in millimeters of BRIDGES' salivary gland drawing (1935). In the third column is given table numbers 2, 3, or 4 in which actual numbers of each hypertriploid obtained are recorded. The three succeeding columns compare body size, wings, and eyes in hypertriploids with their 3X3A, 2X2A sibs and 2X3A sibs. The next column presents the relative fertility of the hypertriploids tested. For example, two hypertriploid females for the region between the points of breakage of translocations T4 and T29 were fertile out

of 31 tested. A fly was not considered sufficiently tested for fertility unless it survived for three days or proved fertile even though it died before the end of the three day period.

Table 6 shows that in general, body size was either not perceptibly different in hypertriploids from their 3X3A sibs or a little smaller, although slight exceptions to this statement occurred. Wing texture was with one exception, the

TABLE 7

Descriptions of hypotriploid females.

REGION LACKING FROM THREE CHROMOSOMES 2	CYTOLOGICAL LENGTH IN MILLIMETERS	TABLE NUMBER	BODY SIZE	WINGS	EYES	FERTILITY
8L	107	2b	Similar to 3X3A sibs.	Similar to 3X3A sibs.	Facets slightly disarranged; eyes slightly narrow.	1 tested and dead before 3 days
8–45	200	3b	Similar to 3X3A sibs.	Similar to 3X3A sibs.	Similar to 3X3A sibs.	1 tested and fertile
45–53	30	3b	Similar to 3X3A sibs.	Similar to 3X3A sibs.	Similar to 3X3A sibs.	Not tested
4–29	132	4b	Similar to 3X3A sibs.	Similar to 3X3A sibs.	Similar to 3X3A sibs.	11 F/19
29–40	57	4b	About size 2X2A sibs.	Similar to 3X3A sibs.	Facets slightly disarranged.	3 F/4
40–30	100	3b	Intermediate between 3X3A and 2X2A sibs; shape squat.	Wings sometimes lifted slightly over back.	Facets sometimes slightly disarranged.	19 F/33
30–34	75	3b	Similar to 3X3A sibs.	Sometimes wings held slightly apart; sometimes extra veins.	In one specimen ocelli missing.	4 F/6
34R	98	2b	Similar to 3X3A sibs.	Wings often crumpled or outstretched; often extra veins.	Facets sometimes slightly disarranged.	5 F/19
6R	69	2b	Some similar to 3X3A sibs; some similar to 2X2A sibs.	Wings slightly outstretched; sometimes crumpled or with extra veins.	Eyes reduced in size; facets slightly disarranged in many.	8 F/15
30R	173	2b	One specimen size 2X2A sib; one specimen a bit larger.	Wings slightly crumpled; held slightly apart.	Facets slightly disarranged.	Not tested
29–30	157	3b	Intermediate between 2X2A and 3X3A sibs.	Wings held slightly apart; slightly crumpled; clipped on medial side.	Sometimes reduced in size; facets slightly disarranged; ocelli often missing.	1 F/7
29–34	232	3b	Intermediate between 2X2A and 3X3A sibs.	Similar to 3X3A sibs.	Similar to 3X3A sibs.	2 F/2
40–34	175	3b	Smaller than 2X2A sibs.	Similar to 3X3A sibs.	Number of facets markedly reduced; facets slightly disarranged.	Not tested

hypertriploid carrying 34R, as coarse as in 3X3A sibs. Wings were commonly held slightly apart. Occasionally wings were crumpled or had extra veins or were slightly clipped at the ends or the medial edge. Eye facets were in each case as large as in ordinary triploids (3X3A), but facets were often slightly disarranged and sometimes reduced in number, giving the appearance of a narrow eye.

Fertility was in some cases approximately normal, but more often it was sharply reduced.

Table 7 gives brief descriptions of hypotriploid females. It is constructed in a manner similar to table 6. Body size in hypotriploid females varied from $2X_3A$ intersex sib size to $2X_2A$ diploid sib size to $3X_3A$ triploid sib size. On the whole hypotriploid females were slightly smaller than hypertriploid females. Wings and eyes were likewise somewhat more affected in hypotriploids than in hypertriploids. Fertility was not well tested in hypotriploid females owing to the small numbers of these aneuploids obtained, but it was sharply reduced in most cases investigated.

The secondary sexual characters of hypertriploid females were not altered in a male direction. Also no change in sexual differentiation was found (or expected) in hypotriploid females. In one hypertriploid, carrying in excess of $3X_3A$ the section between the breakage points of translocations T29 and T34, there was observed in a single specimen a slight rotation of the vaginal plates. In three hypotriploid females for the region between translocations T29 and T30 vaginal plates were found to be slightly rotated. These minor alterations among the many hyper- and hypotriploid females observed could not be interpreted as real sexual shifts.

Detailed descriptions of sexual characters, body size, wing texture, and eyes of hyperintersexes and hypointersexes were recorded for a number of specimen, where these survived, from each experimental cross. Both of these types of aneuploids varied in their sexual characters similarly to their $2X_3A$ sib intersexes, and accordingly, all were grouped according to DOBZHANSKY and SCHULTZ's classification (1934), as tables 2b, 3b, and 4b show. In some cases, wings appeared to be crumpled more than is commonly found among their $2X_3A$ sib intersexes. Eyes of hyper- and hypointersexes were in a few cases more narrow than in $2X_3A$ sib intersexes. From observing the phenotypes of hyperintersexes no discernible shift toward maleness could be deduced. Likewise no perceptible shift toward femaleness occurred in any of the hypointersexes.

In cases where sufficient numbers of hyper- or hypointersexes were obtained, an attempt was made to determine whether or not a minor shift in sex occurred similar to shifts described by DOBZHANSKY and SCHULTZ (1934) and PIPKIN (1940) for short sections of the X chromosome. Since DOBZHANSKY (1930) has shown that temperature changes affect the sex type of ordinary $2X_3A$ intersexes, it was necessary to make homogeneity tests on the euploid $2X_3A$ intersex hatch of individual bottles of each experimental cross before comparing hyper- or hypointersexes with their euploid sibs. The count of bottles was ruled out where euploid $2X_3A$ intersexes were not homogeneous; i.e., certain environmental influences had altered the proportions of the various sex types of intersexes in the particular bottle concerned. This method of ruling out environmental effects on sex types of $2X_3A$ intersexes was used by PIPKIN (1942).

The results of comparing euploid $2X_3A$ intersexes with their hyper- or hypointersex sibs (after eliminating possible environmental effects on sex type) appear in table 8. Hyperintersexes for six different short regions and a hypointersex for one region occurred in numbers sufficiently high to make possi-

ble comparisons by the chi square method of the proportions of individuals belonging to the different sex type groups with those of $2X3A$ sib intersexes.

The first column of table 8 indicates the aneuploid region under investigation. In the case of interior regions, the translocation numbers are given, the aneuploid region being between their points of breakage. In the case of two end regions studied, the letter R means right hand fragment of the particular translocation involved. In the second column appears the phenotype of the $2X3A$ intersex used for comparison with the aneuploid intersex. The third column gives the phenotype of the aneuploid intersex. Column four gives the value of chi square. Next, f indicates the number of degrees of freedom. The

TABLE 8

Comparison of aneuploid intersexes with their 2X3A sib intersexes by means of the chi square method.

ANEUPLOID REGION	PHENOTYPE OF 2X3A SIB INTERSEX	PHENOTYPE AND KIND OF ANEUPLOID INTERSEX	χ^2	NUMBER DEGREES FREEDOM	PROBABILITY TWO SERIES ARE FROM SAME POPULATION	HOMOGENEOUS?
4–29	Wild type	*b* hypointersex	1.1251	4	0.9 >P>0.8	Yes
29–40	Wild type	*b* hyperintersex	2.2939	4	0.7 >P>0.5	Yes
40–30	*b* (black)	*b sp* hyperintersex	3.6711	4	0.5 >P>0.3	Yes
30–34	*sp* (speck)	*b sp* hyperintersex	5.0476	4	0.3 >P>0.2	Yes
30R	Wild type	*b* hyperintersex	1.2570	4	0.9 >P>0.8	Yes
6R	Wild type	*b* hyperintersex	2.0019	4	0.8 >P>0.7	Yes
29–30	*b* (black)	*b sp* hyperintersex	0.9236	4	0.95>P>0.90	Yes

column headed P gives the probability that the two series of numbers compared are homogeneous. The last column indicates whether or not the two series are to be considered as belonging to the same population; i.e., whether or not the two series differ from one another significantly. All homogeneity tests were made by the chi square method developed by BRANDT and SNEDECOR described in R. A. FISHER's *Statistical Methods for Research Workers* (1932).

In each of the seven comparisons of numbers of hyper- or hypointersexes falling into the five sex type groups with their $2X3A$ sib intersexes, the two series compared were found to be homogeneous. That is, the proportions of hyper- and hypointersexes occurring in the five sex type groups and the proportions of their corresponding $2X3A$ sib intersexes do not differ from one another significantly. Thus there is no indication of any minor sexual shift among the six hyper-intersexes and one hypointersex investigated.

DISCUSSION

Although ten short sections covering the entire chromosome 2 were studied in hypertriploids, hypotriploids, hyperintersexes, and hypointersexes, no influence on sex differentiation was found in any of the aneuploids. Likewise longer sections failed to alter sex differentiation in the aneuploids. Either no

male determining sex genes are present in chromosome 2 or they are undetectable by the triploid method of these experiments.

PATTERSON, BROWN, and STONE (1940) found no evidence of sex genes in their diploid aneuploid experiments using the same 2, 4 translocation stocks as were employed in the present author's triploid experiments. This does not mean that such sex genes do not exist, as these authors have pointed out.

If any sex shift should occur owing to autosomal aneuploidy, we expect to find it in hypointersexes for some section of 2 or 3. These are the only autosomal aneuploids in which genic balance is disturbed to a degree comparable with that found in the X chromosome hyperintersexes and hypointersexes. The most pronounced sex shift among X chromosome aneuploids for short sections was found in hypointersexes (PIPKIN 1940). Hypointersexes for short sections of chromosome 2 were found in seven of ten short sections and also in three somewhat longer regions. Although these hypointersexes appeared phenotypically like their sib 2X3A intersexes, only one of them; namely the hypointersex for the section between translocations 4 and 29 survived in numbers sufficient to make a statistical comparison of the proportions of the five sex type groups in hypointersex and control 2X3A sib intersexes. In the case of hypointersexes for the section between translocations 4 and 29, the proportions of the hypointersexes and their sib 2X3A intersexes falling into the five sex type groups did not differ from one another significantly. Thus it is possible that a very slight sex shift among hypointersexes for other sections of chromosome 2 remains undetected for lack of numbers.

A comparison of the cytological lengths of sections of the X and 2 chromosomes investigated for the presence of sex genes reveals clearly the difference in sex potency between these chromosomes. Lengths measured in millimeters of BRIDGES' 1935 salivary gland map of short sections of the X chromosome studied in triploid aneuploid experiments by PIPKIN (1940) are as follows: m5L, 53 mm; m5–9, 35 mm; 9–17, 58 mm; 17–w13, 35 mm; w13–8, 50 mm; 8–4, 70 mm; 4–1B^{8}, 44mm; 1B^{8}–13, 45 mm; 13R, 37 mm. The total length of the X chromosome measured in millimeters of BRIDGES' 1935 salivary gland map is thus 427 mm. Obviously sections of chromosome 2 studied in the present experiments, the cytological lengths of which are given in table 5, are in general twice as long as the short sections of the X chromosome; yet they failed to produce even a slight shift in the proportion of the five sex type groups among hyperintersexes. A section of the X chromosome, w13L, of length 181 mm, was sufficient when added to 2X3A to produce a weakly fertile hypotriploid female. Likewise, w13R, of length 246 mm, produced a weakly fertile hypotriploid female. The same was true for 8L, 231 mm long. The longer chromosome 2 sections studied; i.e., sections 29–30, 29–34, and 40–34, of approximately the same length or longer than w13L, produced hyperintersexes and hypointersexes that did not differ phenotypically from sib 2X3A intersexes. It is clear that whereas X chromosome sections caused a real shift in sex when added to 2X3A, sections of chromosome 2, of approximately the same cytological length or in one case longer failed to alter the sex differentiation of any of the triploid aneuploids.

The phenotype and fertility of the various hypertriploid and hypotriploid females were less affected than in corresponding hyperdiploid and hypodiploid females. These diploid aneuploids occurred as sibs of the corresponding triploid aneuploids and thus could be compared readily. The diploid aneuploids are expected to be altered more drastically by their aneuploidy since their genic balance is more disturbed than it is in the triploid aneuploids. A similar condition was found in X chromosome triploid and diploid aneuploids (PIPKIN, 1940).

Experiments to study aneuploidy of sections of chromosome 3 by the triploid method are in progress. A consideration of the male potency of the autosomes in *D. melanogaster* must await their conclusion.

SUMMARY

A search was made for possible male sex genes or male potent sections of chromosome 2 by means of the triploid method. Males heterozygous for a single 2, 4 translocation and a normal chromosome 2 and also males heterozygous for two different 2, 4 translocations were crossed with triploid females. By the use of suitable recessive gene markers, hypertriploids, hypotriploids, hyperintersexes, and hypointersexes were identified in the progeny. Hypertriploids survived for each of ten short regions of chromosome 2 covering the entire chromosome as well as for four longer regions. Hypotriploids and hyperintersexes survived for nine short regions and the four longer regions. Hypointersexes, although usually surviving in few numbers, occurred for seven short regions and three of the longer regions. No influence on sexual differentiation was observed in any of the aneuploids. A comparison was made of the proportion of individuals falling into the five sex type groups of hyperintersexes for six short regions, and of one short region hypointersex with the sex type proportions of their corresponding $2X3A$ sib intersexes. This comparison by means of reference to the chi square distribution failed to reveal any minor sex shift.

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SPERMATOGONIAL CROSSING OVER BETWEEN THE THIRD CHROMOSOMES IN THE PRESENCE OF THE CURLY INVERSIONS OF DROSOPHILA MELANOGASTER

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INTERCHROMOSOMAL effects of inversions upon crossing over have been described in females of *Drosophila melanogaster* by SCHULTZ and REDFIELD (1943), STEINBERG and FRASER (1944) and by others. The results have usually been increases in the tested chromosome pair, especially near the spindle attachment region. It has not been possible to tell to what extent the increases were of gonial origin in regions where crossing over was very frequent, but in the case of the rarer detachments of attached X chromosomes, which involve crossing over with the Y chromosome, COOPER (1946) has recognized that the clustering of detachments indicated their gonial origin. He found that inversions which increased the proportion of crossover offspring in other experiments did not affect detachments in $\widehat{XX}Y$ females. STURTEVANT (1944) has found that autosomal inversions increase the frequency of primary non-disjunction and decrease the amount of secondary non-disjunction. The present investigation upon males was undertaken to see whether the mitotic crossovers which may be induced in gonial cells of either sex (WHITTINGHILL 1937, 1938) would be affected by inversions.

MATERIALS AND METHODS

Almost all of the crossovers obtained were from the fourth of a series of experiments using various stocks. In this experiment heterozygotes were obtained by reciprocal matings between the third chromosome multiple recessive *rucuca* stock and a balanced second chromosome stock of Curly/"all". The former stock contained the eight recessive mutants shown in table 2. The other stock was chosen because it contained Inversions (2L) *Cy* and (2R) *Cy*. Adult F_1 of Curly and of wild phenotypes were obtained over a period of three days and saved to receive treatment. The males were etherized and placed in gelatine capsules of 0.7 ml capacity for irradiation. A dose of 3000 r units was administered at 140KV and at 20 cm distance through a 4 mm aluminum filter at the rate of 225 r per minute. The flies were then allowed to feed in vials for one day before being mated.

Testcrosses for the study of crossing over in the third chromosome were performed on 17 Curly and 17 wild males by matings to *rucuca* females. From each male nine culture bottles were obtained from the five successive matings by subculturing the *rucuca* females which had been impregnated in each of the first four matings. The matings to new females were made at the end of the first, fourth, seventh, tenth and twelfth days after X-raying. The classifying of the testcross offspring was terminated on the 16th day of each

TABLE 1

Offspring of testcrosses of rucuca, by families.†

PARENT MALE	TOTAL PROGENY	NONCROSSOVERS rucuca	NONCROSSOVERS WILD	CROSSOVERS, BY REGIONS 1	2	3	4	5	6	7
Cy 1	599	149	421	1 —	3 6	—	1 —	— —	—	13 5
No. 2	68	11	57	— —	— —	—	— —	— —	—	— —
3	452	131	318	— —	1 —	—	1 1	— —	—	— —
4	563	166	380	— —	— —	—	2 2	— —	—	— 13
5	519	141	378	— —	— —	—	— —	— —	—	— —
6*	0	—	—	— —	— —	—	— —	— —	—	— —
7	151	25	126	— —	— —	—	— —	— —	—	— —
8	181	48	133	— —	— —	—	— —	— —	—	— —
9	78	20	58	— —	— —	—	— —	— —	—	— —
10	431	88	330	3 —	— —	—	1 9	— —	—	— —
11	11	1	10	— —	— —	—	— —	— —	—	— —
12	0	—	—	— —	— —	—	— —	— —	—	— —
13	503	127	376	— —	— —	—	— —	— —	—	— —
14	81	18	63	— —	— —	—	— —	— —	—	— —
15	379	96	277	— —	2 —	—	1 2	— —	—	1 —
16	422	100	320	— —	— —	—	1 1	— —	—	— —
17	180	41	139	— —	— —	—	— —	— —	—	— —
18*	390	94	282	— —	3 —	—	— —	— 2	—	— 9
	5008	1256	3668	4 0	9 6	0	7 15	0 2	0	14 27
Curly summary:	84 crossovers 1.68 per cent crossovers 17 chiasmata:			2	4	0	6	1	0	4
No. 51	597	221	363	— —	— —	—	4 7	1 1	—	— —
52	782	243	525	10 —	— —	—	2 2	— —	—	— —
53	822	246	541	30 1	— —	—	— —	— —	—	3 1
54	556	180	368	2 3	— 1	—	1 1	— —	—	— —
55	882	279	594	— —	— —	—	4 5	— —	—	— —
56	477	163	299	1 —	— —	—	5 8	— —	—	— 1
57	595	158	437	— —	— —	—	— —	— —	—	— —
58	0	—	—	— —	— —	—	— —	— —	—	— —
59	774	272	495	5 2	— —	—	— —	— —	—	— —
60	502	118	384	— —	— —	—	— —	— —	—	— —
61	579	175	403	— —	— —	—	— 1	— —	—	— —
62	35	6	29	— —	— —	—	— —	— —	—	— —
63	338	84	253	1 —	— —	—	— —	— —	—	— —
64	13	3	10	— —	— —	—	— —	— —	—	— —
65	605	168	424	12 1	— —	—	— —	— —	—	— —
66	288	94	177	— —	— —	—	10 6	— —	—	— —
67	720	235	481	2 —	— —	—	2 —	— —	—	— —
	8564	2645	5783	63 7	0 1	0	28 30	1 1	0	3 2
Control summary:	136 crossovers 1.58 per cent crossovers 20 chiasmata:			8	1	0	8	1	0	2

* After male No 6 was lost in the second mating, an additional male, No. 18, was mated as a replacement.
† Flies showing *ru* are entered in each column to the left, non-*ru* to the right.

culture, when very few flies were emerging. The classification of unusual offspring of mutant or double crossover phenotype and of 38 of the single crossover flies was verified by further breeding. The plan of the three earlier experiments was, in general, the same as the above.

RESULTS

An appreciable number of induced crossovers were not obtained until the rucuca and *Cy*/"all" stocks were used this year. The results of this experiment

are presented in table 1 for each family separately. In each column the class showing *ru* has been recorded to the left and the non-*ru* to the right. Crossovers were found both in the inversion and in the normal series.

The distribution of these crossovers was, as expected, spotty and erratic. Some males had no crossovers among their offspring. One, male No. 53, had a maximum number of 35 crossovers. The highest frequency of crossover offspring was 5.5 percent in the family of No. 66. One of these males had its crossovers in only one region; the other had two regions represented. Exchanges in three regions were found in four males. The greatest variety of crossovers came from male No. 1, who evidenced crossing over in four regions of the chromosome. The family from Curly male No. 18 is remarkable in that the

TABLE 2

Regional distribution of induced chiasmata in males compared with the standard map distances in females.

LOCI	*ru*	*h*	*th*	*st*	*cu*	*sr*	*e*[a]	*ca*
STANDARD MAP INTERVALS	26	17	0.8	6	12	9	30	
Distributions of 37 chiasmata:								
expected from map	9.6	6.3	0.3	2.2	4.4	3.3	11.1	
obtained from males:	10	5	0	14	2	0	6	
28 clustered gonials*	7	3	—	12	2	—	4	
9 solitary gonials*	3	2	—	2	0	—	2	

* A test for homogeneity of the last two lines gave a Chi-square value of 2.46, for which P, with four degrees of freedom, is .65.

three regions of exchange are each multiply represented thus indicating that all the detected crossing over had occurred in spermatogonial cells. That inference is supported by the fact that these crossovers were found in the fifth mating and in the fourth subculture, both of which were started 12 days after the irradiation treatment. Curly male No. 18 was a stand-in for male No. 6, which was inadvertently killed after seven days of sterile matings.

The presence of complementary crossover classes here as in previous reports is one indication of the origin of these exceptional flies by a crossing over type of exchange. However, due to the many gonial cells through which the crossover chromosomes must pass the reciprocal classes of offspring may be very unequally produced. In the extreme, one of the crossover classes may be absent even though the other is large, as in the families of Nos. 4, 18, and 52.

To compare the Curly inversions with the normal chromosomes as to interchromosomal effect the two series have been totaled first on the basis of crossover offspring and then on the basis of the spermatogonial chiasmata necessary to have produced them. In the Curly series of families there were 84 crossovers among 5008 offspring, a frequency of 1.68 percent. In the non-Curly series there were 136 crossovers in 8564 offspring, a frequency of 1.58 percent. However, this does not necessarily mean that chiasmata occurred with these frequencies in males. Because mitotic divisions in gonial cells following a somatic

type of crossing over can reduplicate the crossover chromosomes, only a small number of chiasmata need be postulated. One can see that as few as 17 chiasmata could have produced the crossovers in the Curly families and that 20 chiasmata could have accounted for all recombination phenotypes in the non-inversion series.

The distribution of all 37 chiasmata inferred in this experiment has been compared with the expectations according to the standard chromosome maps in table 2. The crossovers from male show a great excess of chiasmata between the loci of scarlet and curled, which region includes the spindle attachment, and a failure to occur in the larger stripe-sooty region. A separate listing of chiasmata which were each known from but a single recombination fly has been made in table 2. These solitary recombinations might be attributable to meiotic chiasmata, but a Chi-square test showed good homogeneity as to regional distribution of the assured gonials and these solitaries. Also, unpublished comparisons of larger numbers of solitary and of clustered spermatogonial crossovers confirms the view that most if not all of the singly recovered crossovers came from mitotic crossing over.

Aberrant Offspring

There were several kinds of aberrant offspring not given separately in the tables. Four individuals of several double crossover phenotypes need to be explained particularly, since they may have been due to gene mutations or even small deficiencies in the wild third chromosome. One fly showed the recessive scarlet, another was curled, and two from other families were stripe. All four occurred in the cultures and subcultures receiving eggs from the females used in matings from the fourth to the seventh days after the males had been X-rayed, when, significantly, there also occurred one claret and four roughoid flies in still other families. Because these offspring resulted from sperm which were beyond first prophase at the time of irradiation, they have not been called double and single crossovers. Rather they have been added to the wild-type class of non-crossovers of their respective families. Hence tables 1 and 2 record as crossovers only those offspring of crossover phenotype which resulted from matings three through five, *i.e.*, matings begun seven, ten and twelve days after treatment.

Other indications of the effectiveness of the irradiation were the finding of two roughoid-like mutations, a translocation, two triploids, three flies which were mosaic in several parts of the body, and other simpler mosaics. These also have been recorded as wild non-crossovers.

RESULTS OF PREVIOUS EXPERIMENTS ON INTERCHROMOSOMAL EFFECTS

In the first experiment using the Curly inversions 3347 offspring were raised from 14 males which had received treatment at one to three days of larval life. The males were heterozygous for *ru h th st cu sr e*^{s} *Pr ca* and were mated to *st sr e ro ca* females. The irradiation obtainable during the course of one entire afternoon was only 600 r units, so the experiment was altered merely to see whether crossovers could be induced using these inversion stocks, and

the controls were abandoned. It is remarkable that with this low amount of irradiation five crossovers were obtained, in the interval between the scarlet and stripe loci, from four Curly males out of the 14 treated.

A second experiment was then performed with the same stocks but with the irradiation taking place at Duke Hospital to give treatments of 3000 r and 4000 r. Only three crossovers were obtained from the 11 Curly and the 17 straight-winged males which were fertile out of 48 testcrossed flies.

Following failure with the above stocks a third experiment was set up to study induced crossing over in the second chromosome, with and without the *Payne Dfd ca* inversions of the third chromosome. The second chromosome pair of each tested male was heterozygous for the alternated "all" stocks, (*al*+*b*+*c*+*sp*/+*dp*+*pr*+*px*), and the testcross was made to *al b c sp* females. Larvae of ages two to three days and three to four days were irradiated with 3000 r units. Testcrosses to *al b c sp* females were made with 53 males, of which 47 were fertile to at least some degree. No crossovers were obtained either from 20 Deformed nor from 24 non-Deformed males; and only three had any recombination offspring. One normal male produced a single crossover. Two of the Deformed males had one case of gonial crossing over each in producing 103 and 113 offspring, respectively. The irradiation of young larvae thus gave entirely inadequate results in all three experiments. Crossovers were obtained from 7 of the 44 fertile inversion males and from only 3 of 44 non-inversion males. The interchromosome experiments were not undertaken again until this year, when different stocks were used and the heterozygotes were irradiated as adults instead of as larvae.

DISCUSSION

Previous investigations of interchromosomal effects have dealt with crossing over in the sex or sexes where it occurs naturally. The present experiments have searched for such effects in the unusual situation in Drosophila males, where induced crossing over is of a type not often recognized in females without special methods (WHITTINGHILL 1938).

The lack of any detected interchromosomal effect of the Curly inversions upon crossing over in the third chromosome pair is in agreement with the finding of COOPER (1946) that the same inversions, alone or with Cx,D, have no effect upon the frequency of detachments in $\hat{X}\hat{X}Y$ females, which is accomplished by crossing over between the Y and X chromosomes. The clustering of many of the detachments which were obtained indicated that at least some of the exchanges were due to oögonial crossing over rather than to the usual maturation chiasmata. The fact that detachments in females and spermatogonial crossing over in males are not influenced by the inversions tested may be due to the extremely low frequency of crossing over in any one cell, or to a difference between meiotic and mitotic crossing over. The latter will be considered in a later paper. MATHER (1936) in his cytological study of the distribution of chiasmata among the bivalents of single cells found that for high totals of chiasmata there were negative correlations between some biva-

lents, whereas in cells with fewer total chiasmata, interchromosomal effects were smaller or even lacking. The findings of STEINBERG, (1936) STEINBERG and FRASER, (1944) SCHULTZ and REDFIELD (1943), and STURTEVANT (1944) that inversions in females frequently increase crossovers in other chromosome pairs are consistent for a high crossover system. The lack of interchromosomal effects upon rare types of crossing over with some of the same inversions, as reported here and by COOPER (1946), are in agreement with MATHER'S (1936) observations on relatively low exchange gametocytes.

SUMMARY

The presence of the Curly inversions in *Drosophila melanogaster* males heterozygous for *rucuca* and irradiated with 3000 r units had no effect upon induced crossing over. The Curly series produced $1.68 \pm .002$ percent crossover flies and the wild series had $1.58 \pm .001$ percent crossovers in the third chromosomes.

The 220 crossovers recovered came from a much smaller number of chiasmata, as few as 37, of which 17 chiasmata were in the Curly series and 20 were in the structural homozygotes. A few additional crossovers were obtained in three earlier experiments with different stocks after irradiation in the larval stage. Their inclusion makes a total of 24 chiasmata in 61 inversion males as compared with 23 chasmata in 61 normal males.

The lack of interchromosomal effect here in males is consistent with the lack of any effect upon the rare disjunction of attached X chromosomes, which are at least sometimes oögonial, and with a low or zero effect in MATHER'S (1936) observations on nuclei with relatively low total numbers of chiasmata.

Irradiation treatment of larvae with only 600 r appeared to be sufficient to produce four examples of crossing over in males.

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Page 203, three lines from bottom, after "MORGAN, REDFIELD, and MORGAN 1943" insert "MORGAN, STURTEVANT, and MORGAN 1945."

Page 299, lines 5 and 20 from bottom, for "SUMMER" read "SUMNER."

Page 342, legend to figure 1, H, for "six" read "seven."

Page 383, third column of table, for "$\frac{2}{(1-p)^2}$" read "$\frac{2}{(1+p)^2}$."

Page 386, last line, for "$-$" between the two right terms of the equation read "$+$."

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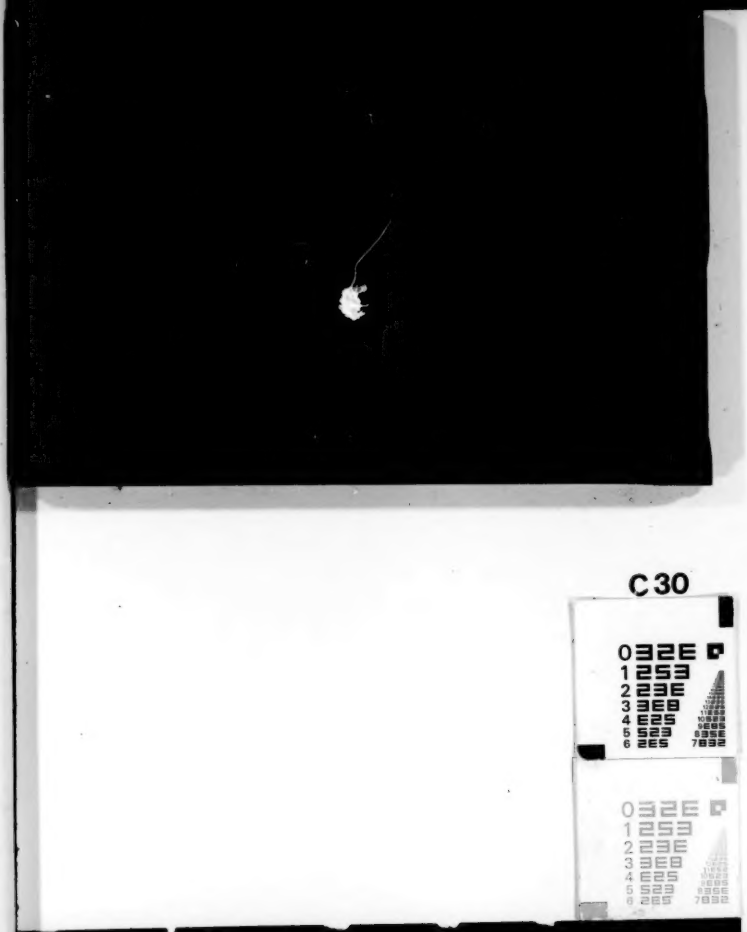
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